# Seed dispersal in isolated North Canterbury forest fragments

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A thesis submitted in partial fulfilment of the requirements for the degree of

Master of Science in Ecology

by

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University of Canterbury

2016

# Abstract

North Canterbury is one of the most severely degraded parts of New Zealand in terms of deforestation, with a large proportion of the lowland area cleared for agriculture. The fragments of native forest that remain are generally isolated and relatively small. These conditions create the potential for a lack of effective seed dispersal due to insufficient frugivorous bird numbers. This project aims to investigate seed dispersal efficacy in these fragments and identify the primary mechanisms behind any dispersal failure. Bird counts, measurement of fruit removal rates and a seedling/sapling dispersion study have been conducted in five fragments. Bird count results show that while bird abundance and diversity vary greatly between sites, two of the most important seed dispersers (bellbirds and silvereyes) are among the most abundant birds in these fragments. The fruit removal data shows that for my indicator species (*Coprosma robusta*) all fruit is being removed by the end of the season. No species were found in the seedling plots that were not previously recorded as present in the reserve, but there were some indications of a shift in composition. There was no significant relationship between numbers of fleshy-fruited seedlings and density of frugivorous bird numbers. The fragments were very different from one another in both bird and seedling composition. The implications of these findings for the persistence of the bird dispersal mutualism in forest fragments are discussed. Investigating seed dispersal processes in one of the most modified parts of the country will not only contribute to effectively managing these fragments but also help to inform conservation efforts in small isolated fragments around New Zealand.

# Acknowledgements

I have a lot of people to thank for helping me out with this project. Firstly my supervisor Professor Dave Kelly who has been so helpful, knowledgeable and always welcoming and ready to help no matter how silly the question. Also to my associate supervisor Professor Jim Briskie for helpful advice and knowledge about birds. Thank you to The Forest & Bird Protection Society and the Canterbury Botanical Society for assistance with funding. Thank you to my five landowners who have kindly allowed me on their land to carry out this research. Thank you to Miles Giller who has been invaluable, liaising with owners and organising site visits but has also been an amazing source of knowledge. Several other people have been fantastic with support and advice, they are Olivia Burge for amazing stats help, Hannah Franklin for support of all kinds, Vaughan Smith for four wheel driving help and accompanying me many times on fieldwork, Channell Thoms my long-suffering office mate and Emma MacKenzie and Tara McAllister for your support network. Thank you to Archie MacFarlane for helping with set-up and with bird call advice. Thank you to Scott Lilly for excellent computer-related assistance. Finally thankyou to my family, every member of which came out on fieldwork with me at least once and especially my father Geoff who also helped with plant identification. Thanks to all my friends and family for your support for which I am very grateful.

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# Chapter 1: General Introduction

## 1.1 The effects of forest fragmentation on biodiversity globally

Widespread deforestation throughout the past two centuries has had severe and well-documented effects on biodiversity around the world. In addition to the plant species that have been lost, the destruction of habitat on such a large scale has resulted in considerable losses of bird species and other forest-dwelling fauna (Brooks et al. 2002, Ewers and Didham 2006). As well as the habitat loss per se, the effects of fragmentation have compounded the problem and continue to affect forest ecosystems in an increasingly fragmented global landscape (Wilcox and Murphy 1985, Andren 1994, Burns et al. 2011). These effects, which are all intertwined, include a reduction in patch size, increased isolation of patches, and an increase of new habitat (Andren 1994, Kupfer et al. 2006).

The change from one large forest to many small patches can have a significant impact on biodiversity. Simply due to probability, a fragment of forest remaining after deforestation of a large area is likely to contain only a subset of the original regional species (Zuidema et al. 1996, Laurance et al. 2002, Cordeiro and Howe 2003). This non-random sampling effect is likely to be especially important in biological hotspots such as the tropics where the initial biodiversity is high (Zuidema et al. 1996). Within the forest fragment, extinction risk is higher than in continuous forest (Burkey 1999), partly because populations in fragments tend to be smaller and small populations are more vulnerable to extinction (Andren 1994, Cordeiro and Howe 2003, Kirika et al. 2008). The extent of the impacts of fragmentation however, is highly context-dependent and is governed by the physical properties of the fragment, the land-use of the surrounding matrix and the traits of and interactions between the species within the fragment.

### 1.1.1 Physical properties of fragments

The size of the fragment is arguably the most important of the physical attributes, with the majority of studies finding that the bigger the fragment, the more abundant and diverse the flora and fauna it supports and the more closely the biota tends to resemble that of continuous forest (Scariot 1999, Hill and Curran 2003, Laurance 2005). When a fragment is very small, the shape becomes important (Hill and Curran 2003, Ewers and Didham 2007). An irregularly shaped fragment has a higher edge:interior ratio than a uniformly shaped one and edges can have a large impact on the ecosystem of the fragment. The effects of edges have been studied and compared all over the world. In early literature it was originally thought that edges were actually beneficial to biodiversity (Ghiselin 1977). They were thought to be the overlap of two habitats where potentially species from both could exist, which can be the case. Edges can also be more productive in terms of fruit sets (McDiarmid et al. 1977, Burgess et al. 2006). Over time though it emerged that edges in reality possessed many characteristics that were detrimental to biodiversity as a whole (Harris 1988, Yahner 1988). When a forested landscape is split into disconnected patches of forest, many plant species that are adapted to the interior of forests find themselves on the edge of a fragment (Fahrig 2003). The effects of the altered micro-climate such as more light, less humidity and greater temperature fluctuations along with the increased vulnerability to wind strike and other stochastic events mean that many plant species suffer or die off and are replaced by more tolerant, pioneer species which are often exotic (Debinski and Holt 2000, Gascon et al. 2000). This change in forest composition also affects the birds, insects and other fauna which rely on the trees for habitat (Laurance et al. 2002). As well as the change in flora, these animal taxa are often affected directly by edge effects themselves in the form of higher predation rates, increased competition from generalist species encroaching from the matrix, and differences in micro-climate (Wilcove et al. 1986, Paton 1994, Stephens et al. 2004, Boulton et al. 2008). Edge effects can permeate into the forest interior and alter the composition and ecosystem functioning significantly. For these reasons, small, irregularly shaped fragments and the species within them are particularly susceptible to edge effects.

In addition to the size and shape of the fragments, the age of the fragment or length of time since isolation is also important. Species decline can be gradual or there can be a delay in the

amount of time it takes for the effects of fragmentation to show. For example, there is often an initial crowding of bird species in a fragment when their habitat is reduced, but over time numbers decline (Bierregaard and Lovejoy 1989, Debinski and Holt 2000, Ewers and Didham 2006). Also changes in population dynamics or forest composition may not be immediately apparent in long-lived species and phenomena such as extinction debt can arise. This occurs when individual members of a species are still alive, but due to inadequate reproduction or recruitment, the current individuals cannot replace themselves and the species will decrease to the point of local extinction (Tilman et al. 1994, Burns et al. 2011, Wotton and Kelly 2011). This kind of lag effect is most often heard of in trees but could potentially occur with some of New Zealand's long-lived birds. The effects of fragment age can be mixed, as sometimes if the dynamics of populations are stable and ecological functioning is maintained, a fragment can begin to recover with time. The effects of edges can also lessen somewhat as they are "sealed" by vegetation, protecting the fragment interior from stochastic events (Matlack 1993, 1994).

The final relevant physical aspect of the fragment is the degree of isolation. The distance between the fragment and other patches or continuous forest can influence the fragment's resilience. When other patches containing resources such as food and nesting places are near it essentially extends the amount of habitat for mobile species, provided they are willing and able to cross the matrix in between (Kupfer et al. 2006). If a fragment is very isolated this can have implications for seed sources and sources of immigration as well as essentially "trapping" some interior-adapted species in a small area, which can lead to extinction or genetic bottle-necks where meta-populations would otherwise mix (Saunders et al. 1991). Recent studies have suggested that the total amount of habitat remaining in a landscape can potentially be equally or more important than the size of the fragments within the landscape (Fahrig 2003, Stouffer et al. 2006). This highlights the importance of looking at fragmentation at the landscape scale as well as the local scale.

Early studies of fragmentation have been dominated by MacArthur & Wilson's "island biogeography" theory (1967) and the follow on meta-population theory (Hanski 1999). It was proposed that island biogeography theory should be applied to forest fragments as they represented islands of biodiversity amongst an uninhabitable "sea" of non-habitat. Therefore

it was argued that they should be governed by the same ecological rules as oceanic islands and species should be constantly turning over, with immigration balancing out extinction and maintaining equilibrium (Levins and Extinction 1970). It became clearer over the years however, that while those theories probably hold true in certain situations, the reality is a lot more complex (Deconchat et al. 2009). For example, the matrix surrounding a forest fragment is unlikely to be completely uninhabitable for all forest species (Andren 1994). Some will be able to utilise it and it will contain its own species that will necessarily interact with the fragment species and may equally use the forest habitat. It has been suggested that it may be better viewed as more of a gradient or continuum of habitat suitability rather than a black and white habitat versus non-habitat situation (McIntyre and Hobbs 1999) and it is now recognised that the surrounding matrix is a key factor in the study of fragmentation (Gascon et al. 1999, Haila 2002, Lindenmayer and Franklin 2002, Kupfer et al. 2006). Diamond et al. (1987) stated that a forest fragment is more like a “mirror” than an “island”, suggesting that the species within a fragment may reflect those of the matrix rather than being isolated forest specialists. This is because the matrix can be a source of generalist invaders that can push out species adapted to the forest interior (Laurance et al. 2002).

The distance the fragment is from other forest as well as the make-up of the land in between also plays a big part in determining the severity of edge effects (Laurance et al. 2002, Ewers and Didham 2006). For example, if the land-use surrounding the fragment is primarily farmland or urban areas then the transition from forest is usually very abrupt and fragment edges are largely unprotected from the elements. If however, the fragment is surrounded by exotic plantation, this can sometimes act as a buffer, lessening the severity of edge effects (Åberg et al. 1995, Denyer et al. 2006, Brockerhoff et al. 2008, Deconchat et al. 2009). If the fragment becomes surrounded by secondary, successional vegetation spreading out from the fragment this should be preferable as it can provide the buffer effect while also being more likely to provide resources to forest species than plantation forests (Arroyo-Rodríguez et al. 2007). Sometimes however, this can actually create problems by displacing large canopy trees and encouraging generalist invaders (Janzen 1970, Benítez-Malvido and Martínez-Ramos 2003).

### 1.1.2 Species traits and interactions:

The resilience of a fragment and the ability of its species to adapt to the physical changes outlined above is dependent on the specific traits that each species possess and upon the mutualisms between them (Ewers and Didham 2006). This varies greatly with different species assemblages and some of these traits and interactions, and their vulnerability or resilience to fragmentation are described here.

The general trend is for more sensitive and specialist species to be the least able to adapt and the more tolerant, generalist species to prevail (Turner 1996, Laurance et al. 2002). Large size in both flora and fauna, low mobility or dispersal capability and potentially high trophic level, among others have also been shown to be traits that can put a species at a higher risk from fragmentation (Turner 1996, Laurance et al. 2000, Henle et al. 2004, Ewers and Didham 2007). Large size usually means larger energy requirements and/or larger home ranges which are needs that are less likely to be met when confined to a small fragment of suitable habitat (Laurance et al. 2002). There are many examples throughout the literature of larger species going extinct first or suffering the most severe impacts after fragmentation events (Turner 1996, Laurance et al. 2000, Meehan et al. 2002, Benítez-Malvido and Martínez-Ramos 2003, Cramer et al. 2007). In the case of trees, the larger, canopy trees are often more susceptible to edge effects and tend to be replaced by smaller, successional species (Laurance et al. 2000). If a large vertebrate species has high mobility they may circumvent this disadvantage, however there are caveats to this. Even highly mobile species will have to expend a lot more energy and potentially increase their predation risk to cross large expanses of open land, both of which are likely to negatively impact on the population (Kupfer et al. 2006). Also, sometimes species that have the technical ability to cover long distances, such as some larger species, or birds that are adapted to the forest interior, will not cross large open areas, or even small gaps due to a fear or avoidance of the unknown or of the lack of cover (Gorchov et al. 1993, Laurance et al. 2002, Cramer et al. 2007). Lastly, often highly mobile species also have larger home ranges which may negate the benefit of mobility (Mühlenberg et al. 1991).

Sometimes taxa that possess traits that should make them vulnerable to the effects of fragmentation can actually thrive due to release from competition or predation by the

extinction or reduction of a fellow species and therefore benefit or even become “hyper-abundant” in a fragmentation situation (Debinski and Holt 2000).

Regardless of the exact species that succumb to fragmentation effects or the ones that benefit, it is clear that community composition following a fragmentation event is likely to be considerably altered, especially at edges. This is not merely a result of some forest species being more resilient and others more vulnerable, it is also a consequence of new species arriving from the surrounding matrix and the traits that they possess as well (Kupfer et al. 2006). Sometimes the species richness can even stay at a similar level as new species take the place of those that have been displaced (Magnago et al. 2014). Whether ecological functioning is maintained however, depends on whether the newcomers can fill the niches of those species that have been lost or reduced, or whether there was enough functional redundancy in a role in the first place (Debinski and Holt 2000, Ewers and Didham 2006).

While the traits that species possess play a major role in the resilience of ecosystem function in a fragmented landscape, the other key factor is the interactions and mutualisms between species – both within the fragment and between forest and matrix species (Henle et al. 2004). It is a fundamental concept of ecology that ecosystems and communities need to be considered as a whole rather than, or in addition to as individual species. For example, even if a species in a hypothetical fragment possessed traits that would technically enable it to tolerate the disruption, it may suffer because an essential mutualist, or more than one, may become extinct or rare (Henle et al. 2004, Cramer et al. 2007). Prime examples of this are usually with essential ecosystem functions such as pollination and/or seed dispersal, without which some plants are unable to effectively reproduce (eg. Federman et al. (2016), Murcia (1996), Cordeiro and Howe (2003), Babweteera et al. (2007)).This can start a cascade of effects longer term (Anderson et al. 2011). If it is a keystone species that becomes extinct an entire forest ecosystem may no longer be able to function as it should.

## 1.2 The role of seed dispersal mutualisms

Mutualistic networks between plants and animals play an essential role in determining and maintaining the diversity of a forest ecosystem. Bascompte and Jordano (2007) even called them the “architecture of biodiversity”. Seed dispersal is one of the most important of these mutualisms, actively shaping the composition of plant communities which in turn influences the forest-dwelling fauna and thus overall biodiversity (Markl et al. 2012).

There are three main hypotheses for the selective benefit of seed dispersal as opposed to seeds merely falling beneath the parent. The first is the “escape” hypothesis (Howe and Smallwood 1982). It was famously postulated by Janzen (1970) and Connell (1971) that seeds have a significantly higher rate of mortality under the parent tree than if they are dispersed. The escape hypothesis states that seeds will have a better likelihood of survival if they “escape” from underneath the parent. The “Janzen-Connell effect” has been expanded to include the many possible reasons for increased mortality that may occur under the parent tree. These issues are mainly related to density-dependence and include competition from con-specifics (Howe and Smallwood 1982, Nathan and Muller-Landau 2000), and increased seed predation, herbivory and pathogen related mortality as a result of the clumping of seeds or seedlings in one place (Packer and Clay 2000, Sekercioglu 2006). The risk of in-breeding is also heightened when seeds are densely clustered under the parent (Willson and Traveset 2000). If seeds can escape, it can help to promote diversity due to the fact that seedlings may be more successful underneath a different species than a con-specific due to a release from competition (Howe and Miriti 2004). The Janzen-Connell hypothesis was originally posited for tropical regions as a potential explanation for the very high diversity in rainforests, and there are a great many tropical examples (Clark and Clark 1984, Peters 2003); but more recently these effects have been shown on several occasions to occur in temperate ecosystems as well (Packer and Clay 2000, Martin and Canham 2010, Wotton and Kelly 2011). Comita et al. (2014) found that Janzen-Connell effects were similar in both the tropics and in temperate regions.

The second proposed benefit of seed dispersal is the “colonisation hypothesis” (Howe and Smallwood 1982). This theorises that dispersal greatly enhances the probability of seeds landing in a tree-fall gap or open habitat that they can then colonise. This theory has become

important in restoration ecology as well, as colonising seeds can be an important tool in recolonising disturbed sites and/or helping to connect patches in fragmented landscapes, especially when dispersed by birds (Ne'eman and Izhaki 1996, Garcia et al. 2010). This type of colonisation can also help to maintain diversity as it can act on different spatial and temporal scales. For example not only can dispersal facilitate the colonisations of distant places where the species has not yet reached but it can also mean that small-seeded, successional species can colonise open ground early and that larger seeded plants will often take longer to arrive but be able to grow well under the shaded canopy (Howe and Miriti 2004).

The third and final hypothesis is the “directed dispersal hypothesis”. (Howe and Smallwood 1982, Howe and Miriti 2004). This poses that plants can have particular mechanisms to ensure that seeds arrive in specific locations favourable for their establishment. An example of this is a bellbird that non-randomly disperses seeds into tree-fall gaps, where the likelihood of success is higher (Wenny and Levey 1998) or with parasitic mistletoes that require their seeds to be dropped on tree branches by birds in order to survive (Reid 1991, Kelly et al. 2007, Whelan et al. 2008). All of these hypotheses assume that any movement away from the parent will generally be beneficial (Howe and Miriti 2004), in line with Janzen and Connell. Janzen-Connell effects are however, very context specific and although there are many examples of evidence of them, there are other occasions where they do not seem to be acting or are cancelled out by other factors. Silander (1978) for example, found that in the tropical shrub *Cassia biflora*, the benefits of clumping in terms of ease of pollination outweighed any potential density-dependence related disadvantages.

Although there are many different modes of seed dispersal, including wind, ballistic systems and passive systems, the majority of woody plant species world-wide are zoochorous or rely on animals for dispersal (Carlo and Morales 2008). The behavioural traits of these dispersers can greatly influence the likelihood of survival and success as a seed but also throughout the different life stages of the plant (Schupp 1993, Schupp and Fuentes 1995). Where a seed is dropped strongly influences the likelihood of seed survival but also seedling survival and even the health and reproduction of the adult tree, should it survive (Peters 2003).

Animals often have distinct patterns of frugivory which influences forest composition in the long-term. For example, birds are more likely to deposit seeds in certain places than in others, for instance under other fruiting trees, which can lead to aggregations of fruiting plants which in turn attracts more frugivores. These inequalities in deposition can contribute to recruitment limitation which helps to maintain biodiversity (Bacles et al. 2004, Clark et al. 2004).

Birds are one of the most important of the seed dispersers, especially in temperate zones where seed dispersing mammals are rare or absent (Sekercioglu 2006, Whelan et al. 2008). On top of the aforementioned benefits for local plant population persistence (Wotton and Kelly 2011), birds are particularly important for long distance dispersal due to their high vagility (Willson and Traveset 2000). Long distance dispersal events are rare but important in terms of colonisation and evolution (Trakhtenbrot et al. 2005). Medium-long distance dispersal is also important for colonising or enriching disturbed and degraded environments and connecting patches of habitat (Garcia et al. 2010).

It has been suggested that seeds can also receive more direct benefits from having been processed by a disperser. There are three ways this could occur; the removal of the outer fruit (de-inhibition), abrasion of the seed (scarification) and the fertilisation of the seed via the faecal material (Traveset et al. 2007). The removal of the outer fruit has been shown to increase germination but empirical evidence for the other two theories is equivocal (Robertson et al. 2006).

The effectiveness and efficiency of birds as seed dispersers can, in the anthropogenically modified world also sometimes exacerbate the problem of invasive weeds. According to Richardson and Rejmánek (2011), over 60% of invasive trees and 40% of invasive shrubs are bird-dispersed. This can cause conservation dilemmas if the invasive plant becomes an important food source for a threatened native species (Buckley et al. 2006).

There is no doubt that frugivorous vertebrates play a vital role in the dispersal of seeds and thus in the regeneration process and maintenance of biodiversity in the forest ecosystem. Moreover, without their input the course of succession would be very different (Bengtsson et

al. 2003). Fewer species would colonise and abiotically dispersed plants would increase (Terborgh et al. 2008). There would also be a heightened risk of invasion by wind-dispersed exotic plants (Bengtsson et al. 2003). For these reasons, the diversity and dynamics of plant communities would likely be significantly altered and regeneration inhibited (Nathan and Muller-Landau 2000, Farwig and Berens 2012).

## 1.3 The effects of fragmentation on seed dispersal

The most obvious way that forest fragmentation can affect seed dispersal processes is by eliminating or reducing animal mutualists that plants depend on to disperse their seeds. When frugivore numbers are severely depleted this means that plants can face much reduced dispersal rates and many fruits are left uneaten which can reduce the reproduction of the plant species. Fortunately, seed dispersal relationships are generally regarded as diffuse mutualisms where many animal species disperse the seeds of one plant and most dispersers interact with more than one plant species (Herrera 2002, Bascompte et al. 2006, Bascompte and Jordano 2007, Whelan et al. 2008). This would suggest that in many cases there is likely to be enough functional redundancy that most plant species in a fragment or fragmented landscape may be robust to extinctions or declines of seed dispersers. When a seed dispersing species goes extinct, often another native species (or several) can compensate for the loss of that particular disperser – or sometimes an exotic species which has arrived can take over the role (Kawakami et al. 2009). However, when it is a fruit specialist that has gone extinct it is often generalist feeders that will fill the gap (Kirika et al. 2008). Sometimes the species that takes over will be a less effective disperser than the one it is replacing. For example, any particular stage in the reproductive process may be maintained at a similar rate, but another may be detrimentally affected by the change in disperser.

Schupp (1993) describes disperser effectiveness as depending on both qualitative and quantitative factors. The quantity of seed dispersal is defined as a) the number of visits made to the plant by a disperser, and b) the number of seeds dispersed per visit. The quality depends on a) the quality of treatment given a seed in the mouth and gut, and b) the quality of seed deposition as determined by the probability that a deposited seed will survive and become an adult. Any alternative dispersers may be deficient in one or more of these aspects.

Differences in behaviour, foraging decisions, habitat preferences and seed processing can result in different patterns of seed deposition and alter the likelihood of successful establishment (McEuen and Curran 2004, Moran et al. 2004, Herrera and Garcia 2010). The distance usually travelled by a new or newly dominant disperser as opposed to an original disperser can also change the likelihood of long distance dispersal (Uriarte et al. 2011). Sometimes, a suite of dispersers can be complementary and losing one means that its specific contribution to the dispersal of the plant is lost. Lehouck et al. (2009) found that an Afromontane tree had a set of three key avian dispersers, dispersing the seeds at different distances depending on their flight behaviour.

As mentioned earlier, large-bodied vertebrates tend to be the most vulnerable to anthropogenically induced extinction. This can affect seed dispersal in two ways. Firstly, larger birds and to some extent mammals, are most often responsible for long distance dispersal (Jordano et al. 2007, Spiegel and Nathan 2007, Wotton and Kelly 2012). For this reason, reductions in large animal species often correspond with reductions in long distance dispersal which can have consequences for colonisation (Uriarte et al. 2011). Secondly, while functional redundancy often means that seed dispersal still functions in severely fragmented areas, albeit at times less efficiently, sometimes anthropogenic interference is such that all of the dispersers of a plant species become extinct from the area and the plant can be left with drastically reduced ability to reproduce. Large-seeded plants are the most at risk of this and often suffer strongly from a decline in large animals, which is related to the fact that the plants require large-bodied animals to disperse large seeds (Cramer et al. 2007). Large-seeded species are often already more vulnerable to fragmentation because they tend to be less tolerant of edge effects (Magnago et al. 2014) and are disadvantaged again by the fact that they are more likely to lose an essential disperser. There are many examples of situations where large-seeded trees have either been left with significantly reduced dispersal or without a disperser at all (Laurance and Bierregaard 1997, Babweteera et al. 2007, Wotton and Kelly 2011, Magnago et al. 2014, Federman et al. 2016). This disproportionate effect of fragmentation on large seeded trees affects forest composition by reducing the recruitment of these plant species but the consequences can also be more far-reaching than that. For example, large-seeded trees are important in successional processes following new ground being colonised. The pioneering, generally small-seeded trees usually colonise first and then

the larger seeded trees come later, facilitated mainly by long-distance dispersal, and are able to establish under the shade of the earlier colonisers (Howe and Miriti 2004). Without the arrival of large-seeded trees (which often tend to be canopy trees) a diverse forest ecosystem cannot be properly established in the site. In addition to being more likely to lose some or all of their primary dispersers, large seeded trees can be less tolerant of edge effects as well and edge environments and small fragments are often dominated by small-seeded successional species (Magnago et al. 2014).

The end result of the reduction of dispersing agents is that zoochorous seed dispersal and/or recruitment is often reduced in fragments compared with other methods of dispersal and compared with continuous forest, and also generally decreases as fragment size decreases (Santos and Tellería 1994, Cordeiro and Howe 2001, Cordeiro and Howe 2003, Galetti et al. 2003, Howe and Miriti 2004, Garcia and Chacoff 2007, Kirika et al. 2008, Whelan et al. 2008, Caves et al. 2013).

## 1.4 The New Zealand context

### 1.4.1 Effects of fragmentation:

New Zealand, like many oceanic islands has an unusual biota that suffered disproportionately from the arrival of humans (Innes et al. 2010). Introduced species brought in over a century ago such as rats (*Rattus spp.),* mustelids, feral cats (*Felis cattus*) and the brush-tailed possum (*Trichosurus vulpecula*) have devastated the native birds (Sanders and Maloney 2002) which have inadequate defences against them, having evolved without mammalian predators (Dowding and Murphy 2001). When coupled with the extensive deforestation carried out by Maori from around 1280 and European settlersfrom1840, the result has been the extinctions of approximately 40% of native land bird species and severe reductions in others (Holdaway 1989). Sadly, while large-scale habitat destruction has decreased, the effects of habitat loss and consequent fragmentation continue to act today, exacerbating the ongoing problem of mammalian predation (Saunders and Norton 2001).

With the exception of some of the country's National Parks, most lowland parts of New Zealand consist of largely agricultural land punctuated sporadically with remnant patches of native forest (Barbaro et al. 2012) or wetland. These fragments vary in their resilience and conservation value but they are important vestiges of biodiversity within the homogeny of human dominated land-use (Burns et al. 2011).

Many of the same effects of fragmentation apply in New Zealand as elsewhere, with ecological functioning of remnants depending on the physical properties of the fragment and on the specific dynamic of the communities within. There are some key differences however between what has been found in the tropics and what has been found in temperate regions. Moreover there are also specific issues faced by fragmented ecosystems in New Zealand that are different from those faced in other parts of the world.

Large mammals are particularly susceptible to fragmentation due to large home ranges and are often the first to go extinct in fragmented tropical forests, whereas they are generally less common or absent in temperate regions (Laurance et al. 2002, Sekercioglu 2006). Furthermore, most studies seem to agree that birds in temperate regions are better at exploiting edges than those in the tropics (Bregman et al. 2014). This has been found to be especially true for frugivorous birds whereas insectivorous birds are more sensitive to edges in both regions (Lindell et al. 2007, Tscharntke et al. 2008). Edges however, can also facilitate species invasions which is a problem that more often occurs in temperate regions. Tropical forest is generally more difficult for invasive species to infiltrate (Fine 2002), whereas in small temperate fragments with high edge-to-interior ratios, edges are more easily penetrated by introduced mammals that abound in the matrix, and by generalist exotic birds which in turn bring invasive plants into the fragment (Norton 2002, Buckley et al. 2006).

Norton (2002) in New Zealand found evidence of edge effects in forest fragments for up to 100 metres depending on which variable was being assessed (eg. microclimate, vegetation effects or predation) and Young and Mitchell (1994) found microclimatic edge effects penetrate around 50 metres in, regardless of fragment size. Young and Mitchell (1994) concluded that forest fragments in New Zealand that are smaller than nine hectares are likely to be dominated by edge patterns and processes.

Pine plantation around or adjacent to forest remnants has been found to act as an effective buffer in New Zealand, both for the reasons it is elsewhere, to protect the forest edge species from changes in microclimate and stochastic events; but also because many (but not all) of the native forest species were able to utilise it as an extension of habitat as necessary (Denyer et al. 2006, Brockerhoff et al. 2008, Deconchat et al. 2009). For many of the more tolerant native birds, including bellbirds (*Anthornis melanura*), tui (*Prosthemadera novaeseelandiae*), kereru (*Hemiphaga novaeseelandiae*), silvereyes (*Zosterops lateralis*), grey warblers (*Gerygone igata*)and fantails (*Rhipidura fuliginosa*), plantation forest surrounding a fragment represented more habitat, less ideal than native forest but preferable to agricultural pasture. Plantations provide canopy cover but don't provide a lot of food for fruit-eating birds and are also generally devoid of the holes some birds require for nesting (Clout and Gaze 1984).

Many of New Zealand's native birds however, are more sensitive than those mentioned above and these are often the most vulnerable to the effects of fragmentation. Hole-nesting birds for example such as the rifleman (*Acanthasitta chloris*) and those that prefer old stands like the New Zealand robin (*Petroica australis*) can be very much restricted to native forest and rarely occur or venture outside of it (Barbaro et al. 2012). Those that are limited in dispersal or require large ranges like kaka (*Nestor meridionalis*) and kakariki (*Cyanoramphus spp.)* suffer similarly (Diamond 1984). As in other parts of the world, the large-bodied species have been the most vulnerable and many of them are now extinct or functionally extinct (Holdaway 1989, Wotton and Kelly 2011). It has been theorised that the birds that have gone extinct in New Zealand's past, possessed certain traits that made them more likely to go extinct and that they had a different set of traits from most of the extant native birds today (Cassey 2001). One of these traits was large body size. One of the few large-bodied forest species left on the mainland, the kereru or New Zealand pigeon is doing comparatively well now that hunting them is illegal and large-scale forest destruction has tapered off. However they, like all of the native bird species are at risk from predatory mammals (Mander et al. 1998). They do have the advantage of being one of the extant bird species that is capable of using the matrix, provided there are enough food resources around, and will eat adventive fruit as well as native if it is in the area (Williams and Karl 1996).

### 1.4.2 Seed dispersal in New Zealand:

New Zealand is unusual in that it has a high number of bird-dispersed trees for a temperate region. Kelly et al. (2010) put the figure at around 60% of all trees. It also has a number of plants that have ornithopholous flowers or are adapted for bird pollination(Kelly et al. 2010). With the forest ecosystem so reliant on birds for ecosystem function and such a depleted avifauna, one might expect these mutualisms to be in dire shape. Approximately 30% of trees are bird pollinated but pollination was for a time not thought to be at risk due to the potential of insects compensating for bird visitations (Clout and Hay 1989, Kelly et al. 2010). Kelly et al. (2010) found that this was not necessarily the case and that pollen limitation had likely been underestimated in New Zealand.

In terms of seed dispersal however, New Zealand's forest plants have proved to be fairly robust in this regard. While higher dispersal rates were found on predator-controlled off-shore islands with a more intact avifauna (Anderson et al. 2006), dispersal limitation does not seem to be a major problem (Kelly et al. 2010); although the potential is there for mistletoes due to the fact that their seeds need to be consumed by a bird to enable germination. The exception to this resilience is the familiar story of large-seeded trees. With kereru being the only large-gaped disperser left in forests, there is potential for dispersal limitation for the native trees with the largest seeds (Wotton and Kelly 2011). Clout and Hay (1989) found that there were 11 species that now rely almost solely on the kereru for dispersal. It has since been found however, that only one of these species (*Beilschmiedia tarairi*) cannot be eaten by any other bird. The others all produce some fruits that are small enough to be eaten by at least the tui. The reason for this is that research has shown that birds are less limited by gape-size than it was previously thought (Kelly et al. 2010). Some birds can consume large fruits by squashing them if they are soft or by extending their gape by stretching. This allows for medium-sized dispersers such as tui or even bellbirds to take the smaller fruits of the large-seeded trees (Kelly et al. 2010). Despite this, the suite of dispersers for these large-seeded trees is still greatly reduced and they are likely to be dispersal limited in some places (Anderson et al. 2006, Kelly et al. 2006, Wotton and Kelly 2011). It also remains to be tested whether there are fitness consequences if the smallest fruits of these trees are dispersed more often than the large ones (Kelly et al. 2010).

The other problem with kereru being the only large frugivore remaining is the effect this is likely to be having on long distance dispersal. Kereru, despite sedentary habits are strong fliers and efficient dispersers which can carry fruit a lot further from the parent tree than any other extant species can (Wotton and Kelly 2012). This helps with colonising new areas, restoring degraded areas and aids regeneration and diversity by helping seeds to escape from Janzen-Connell effects, which have recently been shown to be active in New Zealand's forests (Wotton and Kelly 2011, Jana 2012)

One of the reasons that for most plants dispersal is still functioning adequately is that some of the more tolerant species which are capable of living in small fragments and utilising the matrix include highly frugivorous birds such as kereru, bellbirds, tui and silvereyes (Diamond 1984, Williams and Karl 1996, Kelly et al. 2006). These four species account for the majority of seed dispersal of native plants throughout the country (Kelly et al. 2006). Part of the reason that dispersal limitation isn't more of a problem in New Zealand is that the generalist silvereye, which self-colonised from Australia in 1856, has become a vital and very efficient seed disperser, eating almost every species of fruit small enough for it to eat (Williams and Karl 1996). With the majority of New Zealand's fleshy-fruited species bearing small seeds (Lord et al. 2002), this has likely compensated for some of the lost dispersing species (Kelly et al. 2006, Kelly et al. 2010). Two introduced turdids (blackbird (*Turdus merula*) and song thrush (*Turdus philomelos*) also assist in native plant dispersal (Burns 2012), although the extent of their contribution appears to be context dependent (Kelly et al. 2006, MacFarlane et al. 2016) and likely outweighed by the fact that these two species also disperse invasive weeds (Williams and Karl 1996, Kelly et al. 2006, Wotton and McAlpine 2015, MacFarlane et al. 2016).

While birds carry out the majority of zoochorous seed dispersal in New Zealand, native bats and reptiles are also dispersers of seeds and may have contributed even more in the past, with several species of geckos and skinks playing a part (Whitaker 1987, Wotton et al. 2016). It has been posited that introduced mammals, especially possums and rats (*Rattus spp.*) may also play a small role in seed dispersal (Cowan 1990, Williams et al. 2000) but they are also seed predators which often crush the seeds they eat rendering them unable to germinate (Williams et al. 2000) and can cause high seed mortality, especially under parent trees.

Fragmentation continues to detrimentally alter forest in New Zealand and exacerbate the effects of mammalian bird predation, especially at edges. While many fragments are on private land and not subject to much, if any conservation action (Burns et al. 2011), it is essential that they are retained. This is true for the species which are restricted to native forest, but also for the forest species that are able to exist in this highly modified landscape, provided there are patches of cover and resources connecting habitats together.

The state of the mutualisms between forest plants and their seed dispersers in small fragments is likely to vary depending on context, but is also likely to be considerably more at risk than in continuous forest. Finding out how resilient these fragments are and how the mutualism is functioning within them, as well the mechanisms behind any failure will aid in efforts to conserve both biodiversity and ecosystem functioning in these precious remnants of native forest. It will also add to the pool of knowledge about the effects of fragmentation on bird-plant mutualisms in New Zealand.

## 1.5 Aims and objectives

The objective of this study was to investigate the state of the bird-plant dispersal mutualism in small isolated North Canterbury forest fragments. To determine this I considered three main questions:

1) Are the important dispersing birds present and in sufficient numbers to disperse the fruit? (Chapter 2)
2) Are the birds removing the fruit? (Chapter 3)
3) What does seedling composition tell us about dispersal effectiveness for fleshy-fruited plant species in the fragments? (Chapter 4)

# Chapter 2: Bird abundance and diversity

## 2.1 Introduction

### 2.1.1 Effects of forest fragmentation on avifauna globally.

Fragmentation of forest has been widely shown to have negative effects on the forest avifauna both in the tropics and in temperate regions (Wilcove et al. 1986, Laurance et al. 1998). The main pathways through which fragmentation can affect bird species (other than the effects of habitat loss itself) is through the creation of edges, the reduction or disappearance of food resources, the disconnection of patches of habitat and sometimes a decrease in nesting success (Andren 1994, Robinson 1998, Gascon et al. 2000, Stephens et al. 2004). There are however many factors that contribute to the resilience of a bird community or of an individual species in the face of such disturbance.

Forest fragmentation has been found to influence bird species differently depending on geographic location (Lindell et al. 2007). Studies have at times found mixed results which is likely a reflection of the large variation in species' reactions to fragmentation disturbances. However some patterns have emerged. For example, as a whole it appears that birds in temperate regions are often more resilient to the effects of forest fragmentation than their tropical counterparts (Bregman et al. 2014). It has been suggested that a possible reason for this may be that temperate areas are naturally more patchy than tropical regions and that the native species have therefore evolved the ability to exploit edges or have a higher tolerance for them (Báldi 1996). Moreover, the climate in temperate regions is more seasonal and more changeable in general compared to the fairly stable tropical climate. This may mean that the birds native to temperate regions are more flexible with their resource use as they have had to change resources with the seasons or when a particular food source becomes scarce (Lindell et al. 2007).

Different guilds of birds can also be differentially resilient to the effects of fragmentation. Both in the tropics and in temperate regions insectivores have been found to be less tolerant of edges and small fragment size than other guilds (Stouffer et al. 2006, Lindell et al. 2007,

Tscharntke et al. 2008), but again results are not always consistent (see Watson et al. (2004)). It has been hypothesised that the reason insectivores may be more at risk is due to the fact that the food resources of frugivorous and nectarivorous birds, such as fleshy-fruited plant species, are more likely to grow in gaps and may produce higher flower crops or fruit sets in these conditions (Kelly et al. 2000, Lindell et al. 2007, Magnago et al. 2014). In temperate regions this seems a plausible explanation as studies have found higher frugivore activity at edges and gaps along with the higher food availability (Thompson and Willson 1978, Malmborg and Willson 1988). However in the tropics the pattern is less clear. Restrepo et al. (1999) found that although fruit availability was often still higher in gaps and edges, the frugivorous birds did not seem to react to this which suggested an uncoupling of frugivore behaviour and resource concentrations. This could be attributed to the fact that tropical birds are often unwilling to cross gaps (Laurance et al. 2002). Other tropical studies have found that frugivore activity was indeed higher at gaps and edges (Levey 1988, Galetti et al. 2003), so it appears that further research is needed.

Whichever guild they belong to and regardless of region, specialists and larger-bodied birds are generally less able to cope with the effects of forest fragmentation, or indeed most anthropogenic disturbances (Sekercioglu and Sodhi 2007). In frugivorous birds these traits are inter-linked, with larger bird species more often being fruit specialists where small passerines are more likely to supplement their diet with insects (Cramer et al. 2007). There are many examples of specialist and larger frugivores being the first to become locally extinct following a fragmentation event or on-going landscape fragmentation (Turner 1996). Generalist species are more likely to be able to adapt to the loss of a particular food source by compensating with another. They are also more likely to be able to supplement their diet with food from the surrounding matrix whereas forest specialists may not, due either to a lack of suitable food outside the forest or an unwillingness to venture into open areas (Laurance et al. 2002). When fragments are very small and isolated the distance to find food, nesting sites or a mate may be just too great and often these fragments cannot support some bird populations long-term (Burkey 1999). This is more likely when the species exhibit the traits mentioned above, such as large body size and thus often larger home ranges and resource needs; and specialist needs in terms of diet or habitat requirements.

Stephens et al. (2004) reviewed studies looking at nesting success in fragmented environments and found that in the majority of studies, nesting success was lower near edges than in forest interior and in small fragments than in larger patches. However he found that these differences were more obvious at a landscape scale rather than a local scale. Most studies attributed the reduced nesting success to increased predation of nests and/or increased brood parasitism. In New Zealand, Boulton et al. (2008) found that the nesting success of the North Island robin (*Petroica longipes*) was not significantly affected by edges. The authors proposed two possible reasons for this. Firstly that mammalian predation of birds is so high in New Zealand that this would obscure any potential differences between edges and interiors or small and large fragments. Secondly that most studies overseas have found that it is avian nest-predators that increase at edges more than mammalian ones. While New Zealand retains some avian nest predators (including the Australasian harrier (*Circus approximans*), long tailed cuckoo (*Eudynamys taitensis*), morepork (*Ninox novaeseelandiae*) and kea (*Nestor notabilis*)), the majority of nest predation in New Zealand is carried out by introduced mammals (Innes et al. 2010). In the case of brood parasitism, New Zealand has two brood parasites, the shining cuckoo (*Chrysococcyx lucidus*) and long-tailed cuckoo, however neither of these parasitise robin nests (Boulton et al. 2008).

### 2.1.2 Role of birds in seed dispersal globally.

Seed dispersal is a vital part of the forest regeneration process, with seeds that are dispersed away from the parent plant sometimes having a much higher rate of survival (Janzen 1970, Connell 1971). The act of dispersal is a key process in shaping plant composition and diversity within a forest (Bascompte and Jordano 2007). The abundance and diversity of birds in an area can have a sizeable effect on seed dispersal processes with a large proportion of plant species world-wide adapted for bird dispersal. Bird species differ in their dispersal effectiveness and may be a more effective disperser for one plant species than another. Generally bird-dispersal mutualisms are such that one plant can be dispersed by many bird species and one bird will eat the fruit of many different plant species (Whelan et al. 2008). Sometimes though, more specialist relationships between a plant and its disperser will occur.

Large-bodied birds are perhaps especially important as they are the only ones capable of dispersing large seeds and they are disproportionately responsible for long distance dispersal (Wotton and Kelly 2012). The reason that they are effective at long distance dispersal is that they are usually strong fliers, have larger home ranges and longer gut retention times, especially for large seeds (Wotton and Kelly 2012). Long distance dispersal is important for colonising new areas and is becoming increasingly important as landscapes become more fragmented. Long distance dispersal can help to connect fragments as well as directly begin the process of reforestation (Garcia et al. 2010). Large-seeded trees are also often canopy species so it is important for large-bodied frugivores to deposit these seeds in new areas (Howe and Miriti 2004).

For the reasons outlined above, changes in abundance but also changes in bird communities can greatly alter regeneration processes within an area. If frugivorous bird numbers are reduced or if certain members of the avifauna become locally extinct then some plants can be left with a reduction in dispersal quantity and/or quality (Schupp 1993). Bird abundance is likely to be a suitable predictor of seed dispersal where the avifauna consists of largely generalists whereas diversity of birds may have more of an influence when there are many specialised interactions (Pejchar et al. 2008, Garcia et al. 2010). An important point to consider when using the bird community to assess seed dispersal is that many bird species that are not strictly frugivorous will take some fruit therefore if they occur in large numbers they can also contribute to seed dispersal processes.

### 2.1.3 New Zealand's avifauna.

Historically New Zealand had a large and varied avifauna. There have been many extinctions since the arrival of humans and some of the extant species have a greatly reduced range or have become functionally extinct on the mainland (Holdaway 1989). The introduction of pest mammals such as the mustelids, possums (*Trichosurus vulpecula*), rats and mice (*Mus musculus*), to which New Zealand's native birds have inadequate defences, has meant that species which are particularly vulnerable to them have been severely reduced or become extinct (Dowding and Murphy 2001). For example many New Zealand birds spend a lot of time

on the ground either due to physiology or behaviour (Innes et al. 2010). Many of the endemic species also do not have the ability to recognise mammals as a threat or do not know how to react if they do, having evolved with only aerial predators which require quite a different defensive response (Innes et al. 2010).

The native forest birds that have been resilient enough to still be common in Canterbury forest include the fantail (*Rhipidura fuliginosa*) and grey warbler (*Gerygone igata*) which are chiefly insectivores, the bellbird (*Anthornis melanura*) and silvereye (*Zosterops lateralis*) which feed on insects and fruit, and the kereru (*Hemiphaga novaeseelandiae*) which is primarily frugivorous. Other native birds that are less commonly seen but still present in many patches of forest include the South Island robin (*Petroica australis*), tomtits (*Petroica macrocephala*), brown creepers (*Mohoua novaeseelandiae*) and riflemen (*Acanthisitta chloris*). The former set are likely to cope better with the effects of forest fragmentation whereas the second group often require larger patches of forest as they are less able to use the matrix (Clout and Gaze 1984, Diamond 1984). While tui (*Prosthemadera novaeseelandiae*) are an important seed disperser in New Zealand generally, there are very low numbers of tui in Canterbury despite their high numbers in other parts of the country. They have been absent for a long time and although introductions to Banks Peninsula have been made recently, they are still present in very low numbers and we would not expect them to be making a major contribution to seed dispersal in Canterbury (Schmechel 2009). Most of the other native forest birds are uncommon throughout the country and/or in the South Island.

There are also numerous common introduced birds that occur in New Zealand's forests with frugivores such as blackbirds *(Turdus merula)* and thrushes (*Turdus philomelos*) found throughout the country. Several species of finches, dunnocks (*Prunella modularis*) and starlings (*Sturnus vulgaris*) also use the forest habitat at times but as birds that inhabit open spaces we would expect them to favour edges or small fragments. In the small, isolated fragments in this study we would expect to see the more common native forest birds along with blackbirds, thrushes and starlings; with pasture species common at edges and in the smaller fragments. The most effective suite of seed dispersers that could be present in these covenants would be silvereyes, bellbirds and kereru as these species, along with tui,

contribute the most to seed dispersal in New Zealand (Kelly et al. 2006). An abundance of these species would indicate that adequate dispersers were present in the fragments. Other native species which take fruit occasionally such as fantails, brown creepers, grey warblers, tomtits, robins and riflemen may be contributing if they are present in large enough numbers. Blackbirds, thrushes and starlings if present, would likely also contribute to the dispersal of both native and introduced species. If long distance dispersal was functioning and helping to reconnect the fragments we would expect to see kereru which can spread larger seeds and fly further than the other native species.

This chapter aims to determine what birds are present in the small Canterbury forest fragments, and whether the key frugivorous birds are present in sufficient numbers to effectively disperse the seeds of the forest plant species.

## 2.2 Methods

### 2.2.1 Study sites:

North Canterbury is one of the most heavily modified parts of New Zealand with large areas of forest having been cleared for agriculture. The fragments that remain can be of high conservation value but are often isolated and comparatively small, and most are on private land with little or no intervention.

This research was conducted at five different sites around North Canterbury. All sites were covenanted fragments of native forest of varying sizes. They were on private farmland but were managed by the Queen Elizabeth II (QEII) Trust. They had been grazed in the past but were then fenced off from stock and had been for between one week and 28 years. The forest types varied somewhat but were all typical of lowland Canterbury forest. All covenants were surrounded by pasture. The five sites were chosen based on representativeness, and on the willingness of the owners to allow the research. Site information draws from QE2 North Canterbury representative (M. Giller, pers. comms). and personal observation.

**Taylors Bush:** Area: 8.3 ha Altitude: 320-340m

Taylors Bush was a rare remnant of beech (*Nothofagus solandri)* and podocarp forest with areas of coprosma scrub and wetland situated just south of Coopers Creek village. It had been fenced off from stock for 20 years. It was a uniformly shaped rectangle and generally reasonably flat. It consisted of modified-primary and secondary forest with strong lower tiers. This remnant was botanically diverse and was also home to many notable orchids. The composition appeared to have been well-preserved although there had been recent wind and snow damage with many large fallen trees, and blackberry (*Rubus fruticosus*) was encroaching in the tree-fall gaps. Annual rainfall was higher here than the other covenants.

**Kainsdale:** Area: 2.1 ha Altitude: 40-80m

This was the smallest of the five covenants. It had been fenced off from stock for 28 years. It was adjacent to a pine plantation until recently at which point the timber was harvested and had not been replaced. The covenant was on a steep southwest facing slope with a gully running down the middle. It consisted of secondary vegetation dominated by mahoe (*Melicytus ramiflorus)*, five finger (*Pseudopanax arboreus*) and manuka (*Leptospermum scoparium)* along with coprosma shrubland. The covenant was surrounded by bracken (*Pteridium esculentum*) and matagouri (*Discaria tomatou*). The slope had meant that the effects of the severe drought during 2015 were more apparent with mahoe trees showing visibly drooping leaves. They appeared to recover however with the eventual rain fall in late 2015 and early 2016.

**Glenkens:** Area: 24.37 ha Altitude: 160-360m

This was the largest of the five covenants and had been fenced for 25 years. A gully passed through the middle of the covenant but there was no running water in the gully for most of the duration of this study (probably due to drought). However it was in flood for the last two visits. The covenant was a regenerating podocarp-hardwood forest remnant which also showed some coastal influences. *Coprosma* spp., kawakawa (*Macropiper excelsum*) and kowhai (*Sophora microphylla*) were common. It encompassed some fairly undulating terrain.

There were signs of deer *(Cervus elaphas)* damage with bark-stripping evident in some mature five-finger. There were also signs of pig (*Sus scrofus*) rooting but mostly in open areas.

**Blythe Downs:** Area: 4.08 ha Altitude:140-240m

This covenant was a "Y-shape" branching into two gullies. The northwest gully was fenced off in 1999, while the northeast gully was fenced in 2008 and was accessible to livestock until that time. The lower tiers were noticeably sparser in the north-east gully. It was a narrow and oddly shaped fragment however it consisted of modified-primary totara (*Podocarpus totara*) forest and had several totara trees that post-dated early Polynesian fires. The gullies had very little water in for the majority of the study but in late spring 2015 became wetter.

**Lindon Lea:** Area: 10 ha Altitude: 15m – 107m

This covenant was the newest, with fencing off only being completed in 2015, one week before the commencement of this study. Prior to that, cattle were grazing inside the remnant. Even in the short time since fencing, some regeneration had occurred, especially with the break of the drought in the spring of 2015. The covenant consisted of secondary kanuka (*Kunzea ericoides*) forest with plentiful mahoe and five-finger and lower tiers of coprosma and ferns. The covenant was separated into two blocks (plus a third further inland that was not used for this study).The two blocks were separated by a river which was barely flowing from April to October but became significantly bigger after spring rain. Steeper areas that were less accessible to stock appeared more diverse. There was a little evidence (mostly old) of deer impacts but no obvious pig sign. The owners were getting a mammalian pest trapping programme underway shortly after the end of this study in 2016.

### 2.2.2 Bird abundance and diversity methods.

In order to gain a relative measure of bird abundance I carried out 5 minute bird counts following the method of Dawson and Bull (1975). Between three and ten permanent counting stations were set up in each of the five covenants, depending on size. To ensure

independence, all counting stations were a minimum of 200 m from any other station. Stations were a minimum of 20 m from the edge of the fragment and all habitat types within the fragment were represented. No counts were conducted within 1 hour of sunrise or sunset when birds are known to be more conspicuous. All counts were undertaken by the same observer (myself) to eliminate any variation in observer ability. All birds heard and seen were recorded. No bird was knowingly counted twice. Each station was represented by both morning and afternoon counts throughout the study. Precipitation, temperature range (cold, mild, warm or hot), canopy sun, wind and other noise was recorded and counts were abandoned if conditions were unfavourable, such as heavy rain, snow, strong wind or very loud noise. On rare occasions a station was counted twice in a row but always with a minimum 15 minute break in between to minimise the likelihood of double counting. No maximum cut-off distance was applied and birds that flew overhead were included in counts. Binoculars were used to assist in identification and occasional sound recordings were taken for later confirmation.

Introduced finches were grouped into a single category called “Finch” as their calls are very similar and it was not necessary to separate them as they are all primarily granivores and seed crushers and thus do not contribute meaningfully to seed dispersal. The category included chaffinches (*Fringilla coelebs*), goldfinches (*Carduelis carduelis*), greenfinches (*Chloris chloris*) and redpolls (*Acanthis flammea*). The few birds (mostly flying overhead) that were unable to be identified due to an obscured view were placed in the “Other” category along with non-forest species such as paradise shelducks (*Tadorna variegata*), black-backed gulls (*Larus dominicanus*) and white-faced herons (*Egretta novaehollandiae*).

### 2.2.3 Statistical analysis

Generalised linear mixed models (GLMMs) (with family poisson) were carried out to determine whether sites differed significantly from each other in terms of frugivorous bird abundance. The GLMMs were performed with R Studio Statistical Software version 3.2.1., using library *lme4*. The GLMMs fitted one fixed effect (site) and two random effects: bird count station, and day of the year (to allow for the times when a station was counted several

times within the same day). To determine if the site effect was significant, each bird species GLMM was run with only the random terms and then compared to the GLMM with site plus random terms and the "anova (model 1, model 2)" command in R was used to test the improvement when site was added. The main seed dispersers and most common birds were then tested individually. These were bellbird, silvereye, blackbird, thrush, grey warbler, fantail and finch. Kereru and brown creeper could not be tested due to there being zero of these birds at one or more sites which meant the analysis could not run.

Post-hoc testing was then performed using Tukey tests with package *lsmeans* (Lenth 2016). This was done for frugivorous birds overall and each bird individually to discover where the differences lay. A Nonmetric Multi-Dimensional Scaling (NMDS) ordination was run using the Bray-Curtis distance matrix to determine the dissimilarities between bird compositions at the five sites. This was run in R using the *vegan* library.

## 2.3 Results

Overall 463 five minute bird counts were carried out with 3413 birds encountered. Of these, 2109 were major frugivores (ie. Bellbird, silvereye, kereru, blackbird, song thrush). The total birds were made up of 21 bird species not including the "Finch" category and the "Other category" (Table 2.1). The mean birds per 5 minute bird count over all sites was 7.4. The lowest mean number of birds was at Blythe Downs while the highest was at Taylors Bush (Fig. 2.1). The order of the sites was unchanged when considering only frugivores (Fig. 2.2).

At Blythe Downs, Kainsdale and Taylors Bush the most commonly encountered bird was the silvereye, making up 22%, 26% and 49% of the total birds respectively. Bellbirds were the most common bird at Lindon Lea (48% of total birds) and the brown creeper was most common at Glenkens (33% of total birds). (Table 2.1).

Table 2.1 Total number of birds recorded in 5 minute bird counts at the five North Canterbury sites. The first five species in bold are the major frugivores. Note that the number of 5 minute counts per site varied.

| Bird species | Blythe Downs | Glenkens | Kainsdale | Lindon Lea | Taylors Bush | TOTAL |
|---|---|---|---|---|---|---|
| **Bellbird** | 24 | 120 | 108 | 406 | 163 | 821 |
| **Blackbird** | 6 | 30 | 27 | 40 | 73 | 176 |
| **Kereru** | 32 | 6 | 1 | 15 | 0 | 54 |
| **Silvereye** | 112 | 55 | 120 | 104 | 562 | 953 |
| **Song Thrush** | 32 | 3 | 7 | 26 | 37 | 105 |
| Brown Creeper | 6 | 149 | 2 | 14 | 0 | 171 |
| Dunnock | 5 | 1 | 7 | 3 | 6 | 22 |
| Fantail | 1 | 19 | 22 | 10 | 24 | 76 |
| Finch | 109 | 15 | 83 | 95 | 91 | 393 |
| Grey Warbler | 52 | 32 | 24 | 64 | 50 | 222 |
| Harrier Hawk | 6 | 0 | 2 | 7 | 5 | 20 |
| Kingfisher | 0 | 0 | 0 | 2 | 2 | 4 |
| Magpie | 6 | 2 | 13 | 26 | 50 | 97 |
| NZ Falcon | 0 | 1 | 0 | 0 | 0 | 1 |
| Skylark | 4 | 0 | 0 | 0 | 0 | 4 |
| Sparrow | 2 | 0 | 2 | 1 | 1 | 6 |
| Spur-winged Plover | 2 | 1 | 4 | 6 | 27 | 40 |
| Starling | 5 | 0 | 1 | 1 | 5 | 12 |
| Swallow | 34 | 0 | 0 | 0 | 1 | 35 |
| Tomtit | 0 | 0 | 0 | 0 | 2 | 2 |
| Yellowhammer | 73 | 1 | 21 | 4 | 0 | 99 |
| Other | 9 | 12 | 12 | 27 | 40 | 100 |
| No. of counts | 100 | 71 | 71 | 114 | 107 | 463 |
| Total (all birds) | 520 | 447 | 456 | 851 | 1139 | 3413 |
| Total (major frugivores) | 206 | 214 | 263 | 591 | 835 | 2109 |
| % Frugivores | 40 | 48 | 58 | 69 | 73 | 62 |

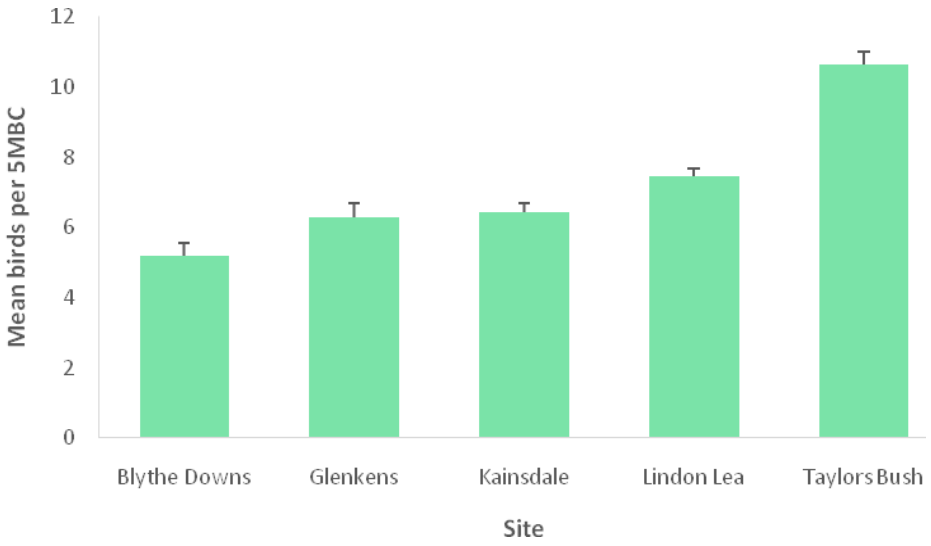


Figure 2.1 Mean (± SE ) number of birds seen and heard per five minute bird count by site.

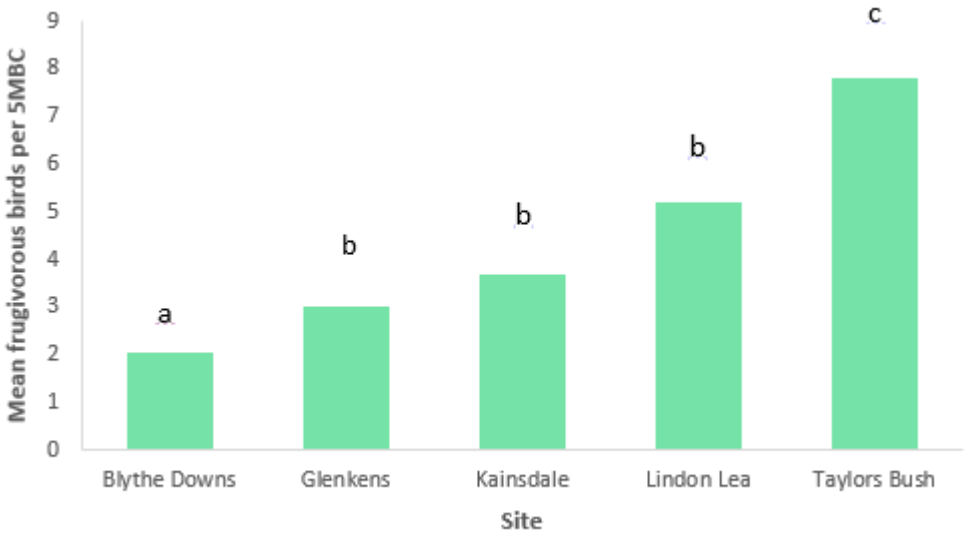


Figure 2.2 Mean (± SE) number of frugivorous birds seen and heard in five minute bird counts by site. Columns not sharing a letter were significantly different according to post hoc tests.

The generalised linear mixed models (GLMMs) showed that the sites were significantly different for frugivorous birds overall and for bellbirds, silvereyes, blackbirds and finches

(Table 2.2). The number of frugivorous birds was significantly higher at Taylors Bush than all other sites and significantly lower at Blythe Downs than all other sites (p values all <0.05) (Fig 2.2).

Table 2.2. Tests for significance of site effect in GLMMs for each bird species (results comparing models with and without the site term).

| **Species** | **Chi Sq** | **DF** | **P** |
|---|---|---|---|
| All frugivores | 57.156 | 4 | <0.0001 |
| Bellbird | 84.017 | 4 | <0.0001 |
| Blackbird | 17.184 | 4 | 0.0018 |
| Finches | 13.921 | 4 | 0.0076 |
| Silvereye | 44.480 | 4 | <0.0001 |

Post-hoc tests showed that bellbirds were significantly higher at Lindon Lea than all other sites and significantly lower at Blythe Downs than all other sites. Silvereyes were significantly higher in Taylors Bush than in all other sites. Blackbirds were significantly lower at Blythe Downs than at all other sites. Glenkens had significantly fewer finches than all other sites. (all p values = <0.05) All other sites were statistically similar (p = >0.05).

The only birds to show an apparent size-related trend were the “finch” category whose numbers increased with decreasing fragment size and perhaps brown creepers which were only found in any number at Glenkens which is the largest fragment (Fig. 2.3).

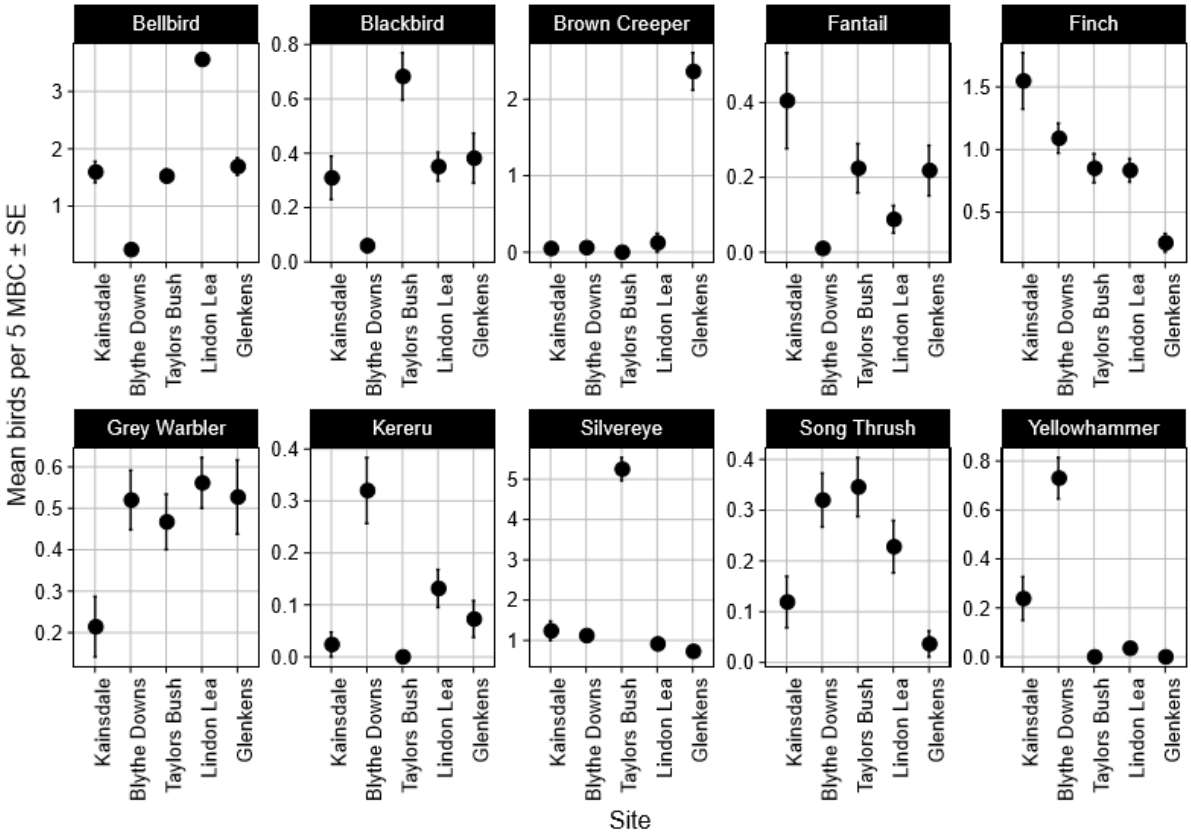


Figure 2.3 Mean number of birds per five-minute bird count by frugivorous/common bird species. Sites are arranged in size order from smallest (left) to largest (right).

Some birds showed changes over the duration of the study. Fantails and silvereyes decreased in the later part of the season whereas yellowhammers, finches and kereru increased. The other relevant species did not display any strong seasonal differences (Fig. 2.4).

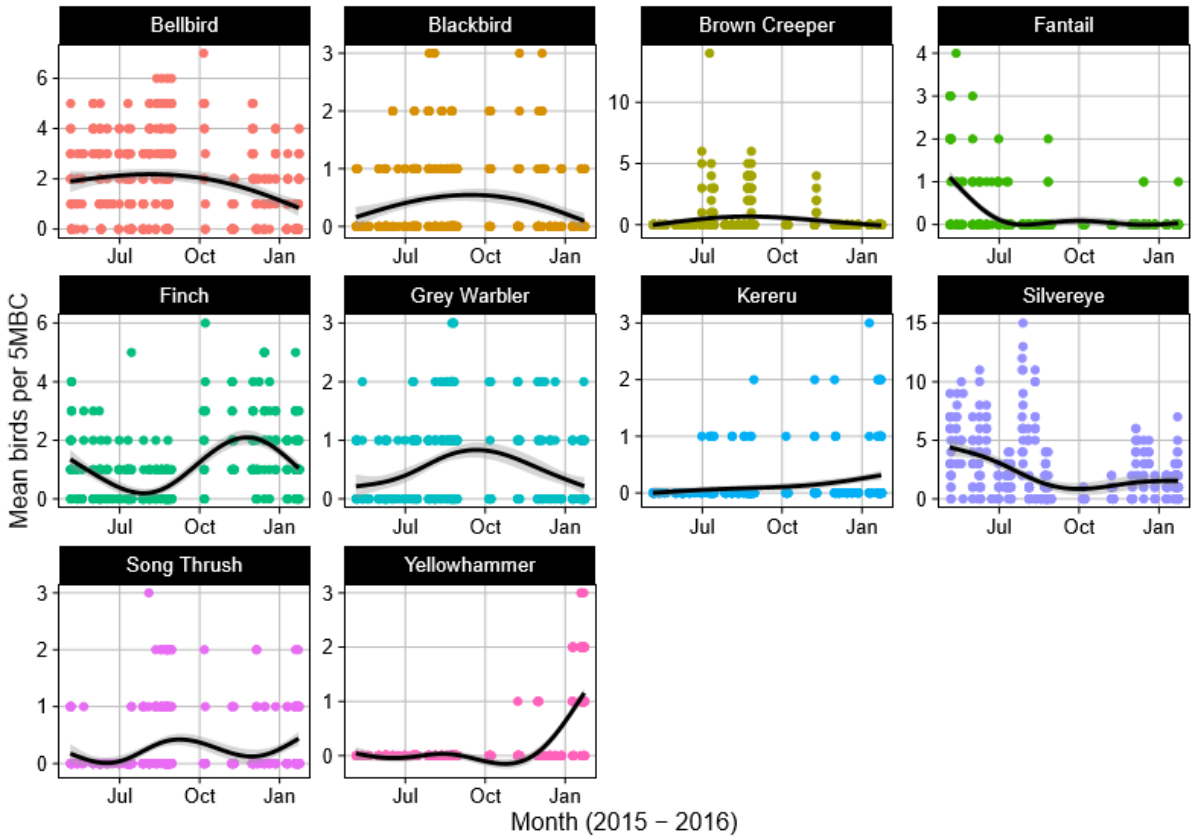


Figure 2.4 Seasonal effects on bird abundance by species. Fitted with a generalised additive model smooth (k = 5) to indicate trends in the data.

The ordination showed there were strong dissimilarities between sites in terms of bird composition with Taylors Bush being characterised by silvereyes, Glenkens by brown creepers, Lindon Lea by bellbirds, Blythe Downs by finches and kereru and Kainsdale by grey warblers and blackbirds (Fig. 2.5).

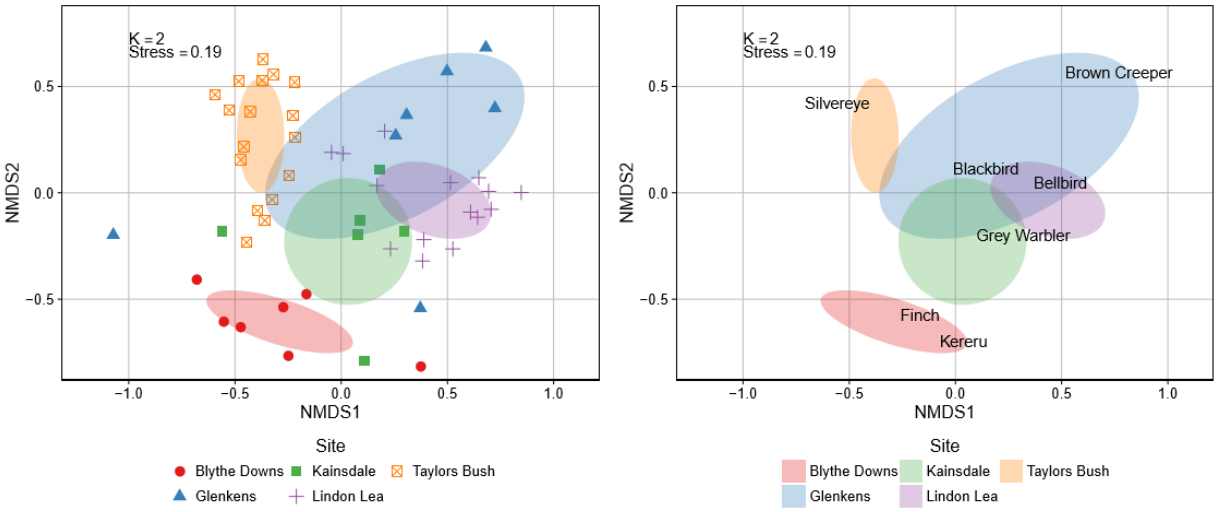


Figure 2.5 Dissimilarities between bird communities at the 5 sites, as shown by NMDS ordination of 463 five minute bird counts. Symbols in the left graph = counting days, birds in the right-hand graph show which birds dominated which sites.

## 2.4 Discussion

Research suggests that bird abundance and diversity should be lower in forest fragments, or fragmented landscapes, than in continuous forest and higher in large fragments than in small ones (Galli et al. 1976, Cordeiro and Howe 2003). The isolation of patches caused by forest fragmentation has also been shown to cause a drop in biodiversity (Laurance et al. 2002). The literature is less clear however, when it comes to the plight of frugivorous birds as opposed to those in other guilds. In temperate regions it has been shown that frugivores are more likely to be able to exploit edges than in the tropics (Sisk and Battin 2002, Lindell et al. 2007, Bregman et al. 2014). There are several cases however, where this has not been the case or where this apparent benefit has been outweighed by other detrimental factors. Large-bodied frugivores are usually affected disproportionately by fragmentation in both regions (Turner 1996, Laurance et al. 2002). In New Zealand, birds that have large space requirements and those that have a strong reliance on forest interior are likely to be the most disadvantaged.

The forest fragments in my study are small and isolated therefore we would expect to see relatively low numbers of frugivorous birds in this study. We would also expect the abundance to decrease with decreasing fragment size. While bird abundances and composition varied a lot between fragments, overall there were more frugivorous birds than expected. In all sites, bellbirds and silvereyes were among the most common birds encountered. Kereru were less abundant, only really being common at two sites (Blythe Downs and Lindon Lea) with strongly seasonal appearances. No kereru were recorded at all at Taylors Bush. This was the most diverse site so the lack of kereru is surprising and may be due to a lack of a source population as this site was the furthest from the other sites. At all other sites at least some were seen during the year which at Lindon Lea and Blythe Downs increased with the fruiting season/rain.

The somewhat low kereru numbers in my study fit with the theory that larger-bodied frugivores are the most vulnerable to the effects of fragmentation (Uriarte et al. 2011), however kereru in New Zealand in general are proving fairly resilient. Kereru are traditionally underestimated in five minute bird counts due to their lack of conspicuousness. They tend to sit silently in trees for large periods of time and can go undetected. For this reason it is possible that kereru abundance in these sites may have been underestimated. This is a distinct possibility in Lindon Lea and Blythe Downs where they were commonly encountered but less likely in the other sites where they were barely recorded in the five minute bird counts and rarely observed at other times during the course of the study. There is however, also the possibility that more kereru arrived in the sites after the study had ended as it was podocarp fruiting season at the time.

On top of the overall high numbers of bellbirds and silvereyes, blackbirds and to a certain extent thrushes were also commonly observed in all sites. These findings suggest that the important seed dispersing birds are present in the fragments, and at some sites in very high numbers. The mean number of frugivorous birds per 5 minute bird count across all sites was approximately four. This is considerably higher than expected. Using the example of bellbirds, Murphy and Kelly (2001) showed an average of just over two bellbirds per five minute bird count on some of New Zealand's off-shore islands and protected areas while in the Lindon Lea fragment I recorded over three bellbirds per count, which is exceptionally high. Taylors

Bush also had very high numbers of frugivorous birds, especially silvereyes of which there were almost as many as there were all other birds combined.

Other than higher than expected bird abundance, the other most noticeable finding from this bird study was the large dissimilarities between sites. Each site had its own distinct bird composition that was quite different from each of the other sites despite the covenants sharing superficially similar characteristics and all being in the North Canterbury region. Lindon Lea was characterised by very high bellbird numbers, Taylors Bush by very high bird abundance and diversity overall, Glenkens by high numbers of brown creepers, Blythe Downs by the large influx of kereru, and Kainsdale by high numbers of insectivores and pasture species.

These strong differences between sites imply that not a lot of mixing is occurring between fragments. Furthermore, the bellbirds had very distinct dialects in each covenant with the Lindon Lea bellbird calls especially distinctive. Bellbirds are known to be able to adapt to the songs of local birds if they immigrate in (J. Briskie pers. comm.) so this does not mean that no mixing at all is occurring but along with the high site dissimilarity in bird species composition it is an indication that each site is more of a distinct habitat island in the matrix than part of a network in the landscape.

The species richness of birds was highest at Taylors Bush, however the diversity of frugivores did not change a lot between sites as bellbirds, silvereyes, blackbirds and thrushes were present in all sites in good numbers and the remaining important frugivore found in this region (kereru) was found in three of the five sites.

Site size did not appear to have a strong effect in this study, with no obvious pattern evident in bird abundance, although there were only five sites. In terms of individual species, the only bird taxa that changed in abundance with site size was the finch category whose numbers increased with decreasing site size. This is expected considering finches are pasture species and it has been shown that the smaller the fragment the more the species composition will resemble the matrix surrounding it rather than be representative of forest interior (Diamond et al. 1987). Brown creepers were only recorded in any number at Glenkens which is the

largest site. The high number of brown creepers at Glenkens was an interesting find as these are less common than the other birds encountered and more restricted to forest, with a preference for old stands (Clout and Gaze 1984). Their abundance could be related to the larger size of the fragment or to invertebrate food resources. The two smallest sites did have the least number of birds and frugivorous birds overall as well as the highest numbers of exotic birds, however Blythe Downs had the highest number of kereru. This was likely due to this site having many totara (*Podocarpus totara*), a favourite food of the kereru (O'Donnell and Dilks 1994), which appeared to draw birds in during fruiting season. The site that had the highest abundance and diversity of birds was Taylors Bush which was moderate in size. This suggests that other factors are having more of an influence on the avifauna in this site. Plant diversity is high at Taylors Bush which could be contributing to higher bird numbers. It is also in a wetter area than the other covenants and is the only one dominated by beech (*Nothofagus solandri*). Beech provides an important source of nectar and some frugivores (eg. bellbirds) are nectarivarous as well.

Some of the birds in this study showed strong seasonal effects. Those with the strongest seasonal differences were kereru, fantail and yellowhammer. Seasonal differences in five minute bird counts can be caused by either a change in abundance or a change in detectability. For the kereru it is likely that the changes were a genuine change in abundance. Kereru numbers climbed sharply over the podocarp fruiting season, especially at Blythe Downs and they are strong fliers that are well-known to follow resources around the landscape as they become available (Clout et al. 1986, Spurr et al. 1992). A large number of kereru arrived at Blythe Downs as the numerous totara trees came ripe although this coincided with an important rainfall event which could have also been a factor. Fantails are known to vary seasonally in local density as they are vulnerable to harsh winters (Spurr et al. 1992). Snow fell at most of the sites over the winter and the fantails decreased at that time in the five minute counts, not reappearing in any number until late spring. This phenomenon is usually caused by the cold and also by snow smothering their insect prey. The change in yellowhammer numbers is more likely to be due to a change in conspicuousness. This change was very marked with no yellowhammer recorded at all until December after which at Blythe Downs, Kainsdale and Lindon Lea they became one of the most commonly recorded species. This is during breeding season when males sing loudly and frequently.

Overall, these results show that the important dispersing birds are present in the covenants in good numbers. Kereru are not common in every site however and as they are both the only disperser of large seeds and likely the most important agent of long-distance dispersal this could potentially have a detrimental effect on seed dispersal. The region of my study did not have any of the large-seeded trees that are found further north such as tawa (*Beilschmeidia tawa*), taraire (Beilschmeidia tarairi) and puriri (*Vitex lucens*). The largest seeded species present was the introduced cherry plum (*Prunus cerasifera*). For this reason the lack of a disperser able to swallow large seeds shouldn't be affecting the forest in these sites. In terms of long-distance dispersal however, low kereru numbers here are more of a concern. Long and medium distance dispersal is especially important in fragmented landscapes, because it helps to reconnect patches and to maintain diversity within remnants. The low numbers or complete absence of kereru in three of the five sites suggests that this may be an issue.

The important findings from this chapter were that there were more frugivorous birds than expected and that the avifauna in the fragments were more distinctively different from each other than expected. Kereru numbers were also low in some sites. These findings imply that there is a sufficient suite of dispersing birds present in the fragments but that long distance dispersal is a potential concern, along with the apparent low level of mixing between fragments.

# Chapter 3: Fruit removal rates

## 3.1 Introduction

Many plants around the world are adapted for dispersal by birds. They produce fleshy fruits which are consumed by the bird and defecated or regurgitated, likely somewhere more suitable than had they merely fallen under the tree. As birds generally forage by sight, the fruits are usually colourful so as to appeal to the potential disperser (Willson et al. 1990). The nutritional value of the fruit for the bird is highly variable and it has been posited that plants employ different strategies for dispersal. Snow (1971) proposed that some tree species produce large and particularly nutritious fruits and fewer of them, while others produce large numbers of small, less nutritious fruits. He proposed that the species that produce large nutritious fruits were adapted for dispersal by specialists that were reliable dispersers, whereas the ones producing small fruits appeal to a wide range of generalist dispersers that tend to be more opportunistic (Snow 1971, Howe 1993). The theory has been further backed up with studies showing that larger seeds often have higher lipid and sugar content than smaller ones and are also preferred by large-bodied, specialist frugivores whereas small seeds are often eaten by many species of generalists (Stiles 1993, Moran et al. 2004).

In New Zealand, there are a high number of small-statured and small-seeded trees (McGlone et al. 2010) and trees with small fruits (Kelly et al. 2010) with the average fruit-size being only 7.7mm (Lord et al. 2002). Correspondingly New Zealand has a volant avifauna skewed towards small birds (Lord et al. 2002). When the silvereye (*Zosterops lateralis*) colonised in 1856 being also small in size, it was able to eat most seeds of the New Zealand vegetation so was thus very advantageous for seed dispersal. The large-seeded trees that are present are often important canopy species both overseas (Howe and Miriti 2004) and in New Zealand (McGlone et al. 2010) and due to their reliance on specialist, large-bodied frugivores, are probably more at risk than small-seeded species (Wotton and Kelly 2011). In all the forest fragments in this study, most of the plant species produce small seeds, so whether there were frugivores present that were large enough to remove the fruits of all trees was not an issue

for this study. However the large-bodied dispersers as well as being important for dispersing large fruits are also important for long distance dispersal (Wotton and Kelly 2012).

Once we have determined whether seed-dispersing birds are present in the fragments we need to investigate whether they are removing the fruit effectively. Dispersal effectiveness can be measured by dispersal quantity and by dispersal quality (Schupp 1993). This chapter examines the former. It aims to investigate whether the fruits of fleshy-fruited species in the fragments are being removed in adequate numbers for regeneration. My aim was to look into whether fruits are remaining on the tree at the end of the season and becoming overripe, or whether a large number of seeds are falling to the ground underneath the parent tree where survival is reduced. Both of these scenarios would imply a lack of adequate dispersal in these fragments. I chose to use *Coprosma robusta* and *Pseudopanax arboreus* to investigate fruit removal in these fragments as they were present in most fragments, occurred in sufficient numbers, have long fruiting seasons and are known to be included in the diets of the bird species that were expected to be present.

Several studies have shown that in temperate regions frugivory can be higher in gaps, at edges, or where the canopy is sparse (Thompson and Willson 1978). These are qualities that these fragments, and forest fragments in general often exhibit. However, fruit removal or dispersal in general is usually dependent on frugivore diversity, frugivore abundance or both (Pejchar et al. 2008, Garcia et al. 2010). Forest fragmentation is known to have the potential to affect both of these (Cordeiro and Howe 2003) . If frugivorous birds were not present in high enough numbers to effectively service the dispersal needs of the fragment or if a suite of dispersers was present that resulted in low fruit removal due to avian behaviour then we would expect to see cases of dispersal failure or reduced dispersal in these fragments. This chapter aims to determine whether birds are removing the fruit sufficiently from the trees or whether it is becoming overripe on the tree or falling to the ground which would show a lack of dispersal.

## 3.2 Methods

### 3.2.1 Study species:

For site information see section 2.2. Between one and six fruiting *Coprosma robusta* plants and one to six fruiting five-finger (*Pseudopanax arboreus)* plants were tagged and monitored for fruit removal. These species were chosen due to their commonness to all sites (with the exception of *C. robusta* being absent at Taylors Bush) and their long fruiting seasons. They also produce fruits that are generally within reach for monitoring. Possibly due to a severe drought in the Hurunui region, the tagged *P. arboreus* plants did not ripen over the period of monitoring. For this reason no data could be obtained on their removal rates. Possibly also drought related was the comparatively low and late fruiting of the *C. robusta* at these sites with fruiting females more scarce than expected and several afflicted with fungus.

Between two and three branches were tagged on every tree and one branch was bagged with a mesh bag to act as a control to test whether undispersed fruits fell off the branches. All fruits present on each branch were counted and whether they were unripe, ripe or over-ripe was recorded. The branches were re-checked on average every eight weeks and the number of fruit at each stage recounted and the bags checked for fallen fruit. All branches were long, thin twigs radiating from flexible branches to minimise the likelihood of mammal interference. The monitoring began in July and continued until no viable fruits remained on the branch.

**Focal species**

**Five finger (*Pseudopanax arboreus*)**

Five-finger or *Pseudopanax arboreus* is in the Araliaceae family. It can grow up to 9 m tall and is widespread in lowland forests. The plants are dioecious but are highly variable and flowers of both sexes can occur in the same inflorescence (Burrows 1995). The fruits are purplish and flat when unripe and become darker and plumper as they ripen. Each fruit contains two seeds. Fruiting season is variable.

**Karamu (*Coprosma robusta*)**

Karamu or *Coprosma robusta* is a large-leaved coprosma and a member of the Rubiaceae family. It is a dioecious shrub, which is early successional and can grow up to about 5-6 m tall. It is widespread in lowland forest throughout New Zealand. Karamu has a long and variable fruiting season with fruits appearing anywhere from April to August and can take up to one year to ripen (T.E.R.R.A.I.N 2015).The ripe fruit is a small, juicy orange drupe that usually contains two seeds(Burrows 1995). The fruits are a preferred food of bellbirds and are also frequently eaten by other frugivorous birds (Williams and Karl 1996).

### 3.2.2 Statistical analysis

The data was limited for this chapter due to non-ripening of *P. arboreus* fruit and late ripening of *C. robusta* causing it to coincide with lambing, which resulted in longer than intended monitoring intervals. This restricted the analyses available. The percentage of fruit removed for each period was calculated as a function of the number of fruits that were available to be eaten during that time interval, (ripe (but not overripe) fruit that remained on the tree at the end of the previous interval) From this, a daily removal percentage was obtained. Due to data limitations only Lindon Lea and Kainsdale could be statistically compared to one another. They were compared with a two tailed t-test assuming unequal variance. A simple linear regression was used to determine whether daily fruit removal percentage was dependent on mean number of frugivorous birds per site. Analysis was carried out in Microsoft Excel 2013.

## 3.3 Results

Overall, 908 fruits were counted on 34 tagged branches on 13 *C. robusta* trees (Table 3.1). Nine of these branches were used as controls. Two from a possible 145 fruits were recovered from the mesh bags that were used as controls.

Table 3.1 Number of trees and branches of *Coprosma robusta* at each site and check dates (number of fruits in brackets).

| | **No. of trees** | **Open branches (fruit)** | **Bagged branches (fruit)** | **Month of setup** | **Check 1** | **Check 2** | **Check 3** |
|---|---|---|---|---|---|---|---|
| Blythe Downs | 4 | 4(52) | 2(7) | 15 July | 26/27 August | 8 November | NA |
| Glenkens | 1 | 2(27) | 1(9) | 23/27 August | 10 November | 31 January | NA |
| Kainsdale | 2 | 8(353) | 0 | 14 July | 13 October | 11 January | NA |
| Lindon Lea | 6 | 11(303) | 6(125) | 18/19/25 August | 7 October | 1 December | 28 December |

Almost all fruits from tagged (unbagged) branches were removed by the end of the season. Five branches had all of their fruits removed in the first interval. 100% of the fruits at Glenkens and Kainsdale were removed and 96.4% and 97.5% for Lindon Lea and Blythe Downs respectively (Table 3.2). A total of three fruits remained on the trees at Blythe Downs at the last check and eleven at Lindon Lea. They were overripe to the point of shrivelled husks. The highest overall daily removal percentage was at Blythe Downs (Table 3.2). There was no observable pattern over time with fruit removal rates with two sites being slightly higher in the first interval and two being higher in the second. Lindon Lea, which was the only site still with viable fruit requiring a third check had a higher daily fruit removal percentage in the third interval (Table 3.2).

Table 3.2 The percentage of available fruit (not unripe or overripe) that were removed from the sites at each interval and the total removal percentage at the end of the season.

| | **Mean daily removal % for first check period** | **Mean daily removal % for second check period** | **Mean daily removal % for third check period** | **Mean daily removal % overall** | **Total % of fruit crop removed by end of season** |
|---|---|---|---|---|---|
| Blythe Downs | 1.95 | 1.35 | NA | 2.6 | 96.25 |
| Glenkens | 0.76 | 0.87 | NA | 0.82 | 100 |
| Kainsdale | 1.03 | 1.10 | NA | 1.1 | 100 |
| Lindon Lea | 1.56 | 1.40 | 3.74 | 2.2 | 96.4 |

The results of the t test show that daily fruit removal percentages at Kainsdale and Lindon Lea were not significantly different from each other ($t = -0.311$, $df = 3.83$, $p = 0.77$). There was insufficient data to make comparisons between the remaining site pairs.

The linear regression showed that fruit removal rate did not significantly depend on the mean number of frugivorous birds at a site ($F = 0.03$, $df = 1,8$, $p = 0.88$ $r^2 = 0.0031$).

As the data are so limited however, these results should be viewed with caution.

## 3.4 Discussion

Almost all fruits were removed from the *C. robusta* trees by the end of the season. The few that remained were very overripe, dry and shrivelled and represented 1.9 % of the starting number of fruits. With the exception of two, fruits in bags all remained on the branches, showing that fruit disappearance in the open treatment most likely represents genuine removal rather than passive detachment.

The low number of fruits remaining on the plants show that most available fruit on this species is being removed and that *C. robusta* in these covenants appears to be being sufficiently dispersed. Although this is only one species, these findings are likely to give us an indication of the likelihood of fruits being removed in other fleshy plant species present in the covenants. Most of the remaining frugivorous birds that are found in this region are generalist in diet and so if they are eating the *C. robusta*, they are likely to be eating most fruits that are present. *C. robusta* has been shown to be a preferred species for the bellbird however (O'Donnell and Dilks 1994, Williams and Karl 1996) which may mean that it is better removed than some others, especially in sites with high bellbird numbers such as Lindon Lea. From the limited data, comparing between sites is difficult but Blythe Downs had the highest daily removal percentage in this study. Whether this is a genuine higher rate of removal is uncertain but it does fit with the fact that Blythe Downs had the highest number of kereru which are the most frugivorous of the regional species and capable of consuming a larger amount of fruit. This site also however, had the lowest numbers of frugivorous birds. Factors that could be affecting fruit removal in these sites include frugivorous bird numbers (although this was not statistically significant with this data), canopy density, fragment size and the land-use of the surrounding matrix. The physical properties of the fragments can affect fruit removal by altering frugivore dynamics.

Forming hypotheses about fruit removal in these fragments is challenging as there are logical reasons to expect it to be low and also to expect it to be high. Fragmentation has been widely shown to interfere with seed dispersal mutualisms (eg. Cordeiro and Howe (2001)). It can affect seed dispersal both directly, by reducing frugivore numbers, and indirectly, by replacing effective dispersers with less effective ones. Conversely, research has also shown that sometimes, especially in temperate regions, frugivory can actually be higher at edges, in gaps and under sparse canopies (Garcia et al. 2010). This would suggest that seed dispersal in fragments may be more resilient than some other ecological processes. Importantly however, such a scenario is likely to benefit specific species, both of bird and plant, more than others. For example, *C. robusta*, the indicator species used in this study is an early successional species that is comparatively tolerant of disturbance. It is also hardy and produces ample, appealing fruit that is fed on by many species of bird. It grows well in gaps and edges where frugivorous activity can at times be higher (Malmborg and Willson 1988). Generalist bird

species will likely also benefit if there are increased food resources from early successional species but only if they too are tolerant of the fragmented conditions. Interior adapted plants and large-seeded plants will also likely be disadvantaged rather than advantaged by the effects of fragmentation. Additionally more specialist bird species or those that are adapted to the forest interior may find less food resources in a fragmented environment where their favoured plant species are reduced or absent as a result of edge effects or other effects of fragmentation. Such imbalances can change seed dispersal processes and thus alter the trajectory of future forest composition – and biodiversity as a whole.

In New Zealand, Barbaro et al. (2012) found that the extant common native forest birds tend to exhibit a fairly neutral response to fragmentation due to their generalist diets however, he found that the self-colonised silvereye was the only species to actually prefer edge habitats. As the silvereye is one of the most important seed dispersers in the country currently, this could benefit seed dispersal of edge tolerant native plant species in fragmented areas.

In these fragments, fruit removal seems to be functioning sufficiently, at least for *C. robusta* which implies that other species may be being sufficiently dispersed as well, especially as most of the frugivores in the region consume the fruit of many species. However, as *C. robusta* is a species which grows well in fragmented forest we need to be a little careful when extrapolating to other plant species, especially forest interior species which would not benefit from any increased frugivory at edges.

# Chapter 4: Seedling study

## 4.1 Introduction

Fragmentation can have profound effects on the composition of the forest vegetation remaining in the landscape. There are several potential pathways for this to occur. Firstly, anthropogenic disturbances such as fragmentation tend to favour small-seeded successional species that are adapted for colonisation (MacFarlane et al. 2016). These are usually short-statured sub-canopy trees and lianes (Tabarelli et al. 1999, Burns et al. 2011, MacFarlane et al. 2016). This can often be at the expense of canopy trees and thus has the potential to alter composition considerably (Benítez-Malvido and Martínez-Ramos 2003). The mechanism behind this occurrence is that fragmentation creates edges and importantly also increases the likelihood of treefall gaps due to the increased mortality of mature canopy trees (Laurance et al. 1998, MacFarlane et al. 2016) Sunlight-loving pioneer species quickly colonise edges and gaps and inevitably penetrate further throughout the fragment. When a fragment is small, irregularly shaped, or both, then this phenomenon is more likely due to the high edge to interior ratio and the higher likelihood of wind damage to existing trees (Arroyo-Rodríguez et al. 2007). Fragmentation also increases the risk of invasion by introduced species which often display the characteristics mentioned above such as short lifespans and a tendency to be light-preferring, and can also be prolific seed producers (Kupfer et al. 2006).

The literature is somewhat contradictory in terms of which modes of dispersal make a species more or less vulnerable to fragmentation. Several studies have found that fragments compared to continuous forest, and large fragments compared to small ones favour wind and other abiotically dispersed plant species over those that are zoochorous (Tabarelli et al. 1999, Cordeiro and Howe 2001, McEuen and Curran 2004). The fact that these plants rely on animals to disperse their seeds and that those animals themselves have the potential to be affected by fragmentation means there should be a higher risk for animal dispersed plants. Other studies however, have found that animal dispersed species were advantaged in fragments (Thompson and Willson 1978, MacFarlane et al. 2016). This disparity implies that there are other context-related factors influencing species vulnerability or robustness to the

effects of fragmentation. Geographical differences and differences among plant species in the same guild are likely to account for this. For example fleshy-fruited pioneer species can favour edges and gaps and thus also small fragments and do well with their wide suite of dispersers (Magnago et al. 2014, MacFarlane et al. 2016), whereas large seeded fleshy-fruited trees and specialists are particularly vulnerable to the effects of fragmentation and often decline due to loss of dispersers and disproportionate mortality (McEuen and Curran 2004, Cramer et al. 2007).

Such changes in the composition of the forest inevitably lead to corresponding changes in the fauna that inhabit the fragment, although determining the order in which faunal changes and vegetation changes occur is somewhat circular and probably also context dependent. Both the plants and the animals can be directly affected by fragmentation and both can influence the other. For example, a decrease in fleshy-fruited plants could be caused by a reduction in bird dispersers but less fleshy-fruited plants to provide food for birds could equally cause a decline in frugivorous birds. Whichever occurs first however, it has been shown widely in the literature that fragmentation can reduce the abundance and diversity of seed dispersers which can have long term consequences for forest regeneration(Herrera and Garcia 2010). Long distance dispersal is also affected by fragmentation due to the fact that many dispersing species are incapable or unwilling to traverse the open space between isolated fragments and thus seed deposition can remain primarily local (Cramer et al. 2007, Uriarte et al. 2011).

The recruitment stage for seedlings can also be affected by fragmentation. Recruitment can be influenced by dispersal effectiveness, for example if the seed is dropped into harsh conditions then the likelihood of survival into adulthood is decreased (Schupp 1993) or if seeds or seedlings are clumped together there can be an increased risk of seed predation (Janzen 1970). Saplings can also experience increased mortality due to ungulate browsing.

The effects of fragmentation on seedling composition appear to be due largely to two key factors – fragment size and isolation. Many studies have found fewer seedlings and/or fewer species of seedlings in fragments compared to continuous forest (Reid 1991, Cordeiro and Howe 2001) and in small fragments as opposed to large ones (Cordeiro and Howe 2001, Wotton and McAlpine 2015). As well as declining abundance and diversity of seedlings, it is

clear that the composition is also likely to be considerably altered over time as the effects of fragmentation continue to act. Small-seeded successional species are likely to become more dominant and canopy trees will often suffer reduced dispersal and recruitment. Invasive species are also more likely to invade. The fauna within the fragment will reflect the changes in the vegetation and thus have the potential to hasten the compositional changes further. All of these changes are time dependent. There is often a significant lag in the time it takes for the effects of fragmentation to show, especially in the case of long-lived trees (Tilman et al. 1994, Wotton and Kelly 2011) Moreover, if a fragment has been previously grazed and is recovering (like all of the sites in my study), the length of time since fencing will likely be important in seedling composition as plant species are differentially affected by grazing and recover at different time scales (Burns et al. 2011).

Fragmentation effects that we might be expected to see in the small and isolated North Canterbury fragments of my study may include low abundance and diversity of seedlings in general - decreasing with fragment size, high numbers of successional sub-canopy species and small-seeded pioneer species as opposed to canopy species, and high numbers of introduced species. At the sites where abundance of seed dispersing birds is low, we would expect relatively more wind- and abiotically dispersed seedlings. Sites that have been most recently grazed should have higher numbers of unpalatable seedlings relative to those favoured by cattle. The effects of isolation mean we would expect novel species to be rare due to reduced long-distance dispersal. They could also mean we may expect variation among sites to be high due to isolation.

The aims of this chapter were to determine whether any seedlings of novel species were recorded (i.e. seedlings present where no adult is known from that fragment), which would indicate long distance dispersal; to investigate any potential changes in plant composition (by comparing seedling abundance and canopy abundance), and to get an indication of whether fleshy-fruited plants were being recruited in the fragments.

## 4.2 Methods

For site information see section 2.2. Existing vegetation at each site was drawn from species lists provided by QE2 North Canterbury representative Miles Giller (M. Giller pers. comm.). To measure the seedlings present in the five fragments, I counted seedlings in repeated small plots at each site. A total of 240 seedling plots were carried out in the covenants (Taylors Bush 40, all others 50 each). This was done using a 0.5 x 0.5m quadrat which was placed randomly every 10-20 metres along the bird counting trail. Quadrats were alternately placed left and right to avoid sampling the often walked route. All seedlings that had sufficient true leaves (i.e. beyond cotyledons) were identified and recorded as well as all saplings. No maximum height threshold was used however saplings taller than one metre would have been excluded due to the method of placement. Seedlings without true leaves were not recorded as definitive identification was not possible. Seedling height category (<30cm or >30cm) was also recorded. Where a species could not be identified in the field, either a photo or small specimen of the plant was taken for later identification by a specialist botanist to ensure correct identification.

### 4.2.1 Statistical analysis:

One way ANOVAS were used to test for differences in mean seedlings per plot by site and mean fleshy-fruited seedlings per plot by site. Tukeys post hoc tests were then performed to establish where the significant differences lay. A simple linear regression was run to determine the relationship between fleshy-fruited seedlings per plot and mean frugivorous birds per 5 minute bird count.

A GLM with binomial distribution was used to test whether the proportion of fleshy-fruited seedlings per plot was dependent on the mean number of frugivorous birds per 5 minute bird count and if so to what extent. All statistical analyses were conducted using R Studio Statistical Software, version 3.2.1.

## 4.3 Results

Overall 1328 seedlings were found from 240 plots. These consisted of 51 different species, 38 of which are fleshy-fruited species. Of the 51 species, seven were exotic (Table 4.1). No species were found as seedlings that were not already recorded as present in the sites at the last survey. The mean number of seedlings per plot was highest in Taylors Bush (10.2+-SE 2.0), followed by Glenkens (5.9+-SE 0.8), Kainsdale (4.8+-SE 1.2), Lindon Lea (4.1+-SE 0.6) and Blythe Downs (3.4+-SE 0.6). If non fleshy-fruited seedlings were excluded the order of the sites remained the same (Table 4.1). The proportions of seedlings that were fleshy-fruited in each site were as follows: Kainsdale 89%, Glenkens 80%, Taylors Bush 65%, Blythe Downs 56% and Lindon Lea 49% (Table 4.2). At both Blythe Downs and Lindon Lea the most abundant seedling species was *Parsonsia heterophylla* which made up 43% and 34% of the total seedlings respectively. *Pseudopanax arboreus* was the most abundant seedling species at Glenkens (23%) and Kainsdale (64%). The most abundant seedling species at Taylors Bush was *Nothofagus solandri* which comprised 24% of the total seedling species found at the site. It is worth noting that *Coprosma* species (especially *Coprosma propinqua*) were well represented in all sites and made up ~20% of all species found across all sites. From a diversity perspective, Taylors Bush had the highest species richness with 25 species (despite having ten fewer plots than the other sites) followed by Glenkens (23), Lindon Lea (21), Blythe Downs (15) and Kainsdale (12) (Table 4.2).

Table 4.1 Plant seedlings present in each site

| | Blythe Downs | Glenkens | Kainsdale | Lindon Lea | Taylors' Bush | TOTAL |
|---|---|---|---|---|---|---|
| *Aristotelia serrata* | | | | 2 | | 2 |
| *Calystegia tuguriorum (nf)* | | 6 | | | | 6 |
| *Carpodetus serratus* | 14 | 1 | | | 1 | 16 |
| *Clematis paniculata (nf)* | | | | 1 | | 1 |
| *Coprosma crassifolia* | | 6 | 8 | 20 | | 34 |
| *Coprosma propinqua* | 22 | 42 | | 23 | 47 | 134 |
| *Coprosma rhamnoides* | | 8 | 2 | 13 | 18 | 41 |
| *Coprosma rigida* | | | | | 15 | 15 |
| *Coprosma robusta* | | | 13 | | | 13 |
| *Coprosma rotundifolia* | | 2 | | | 1 | 3 |
| *Coprosma tayloriae* | | 1 | 1 | | 22 | 24 |
| *Coprosma x cunninghamii* | | 1 | | | | 1 |
| *Cordyline australis* | 1 | 2 | | | | 3 |
| *Dacrycarpus dacrydioides* | | | | | 2 | 2 |
| *Elaeocarpus hookerianus* | | | | | 37 | 37 |
| *Griselinia littoralis* | | 1 | | | 6 | 7 |
| *Haloragis erecta*(nf) | 1 | | | | | 1 |
| *Hebe salicifolia*(nf) | | | 1 | | | 1 |
| *Helichrysum lanceolatum* (nf) | | | | 3 | | 3 |
| *Kunzea ericoides*(nf) | | 3 | | | | 3 |
| *Leptospermum scoparium*(nf) | | | 6 | | | 6 |
| *Leucopogon fasciculatus* | | | | | 2 | 2 |
| *Lophomyrtus obcordata* | | | | 2 | 2 | 4 |
| *Macropiper excelsum* | | 23 | | 1 | | 24 |
| *Melicope simplex* | | 6 | | | | 6 |
| *Melicytus ramiflorus* | 6 | 9 | 6 | 4 | | 25 |
| *Muehlenbeckia australis* | 6 | 8 | 14 | 10 | | 38 |
| *Muehlenbeckia complexa* | 4 | | | | 24 | 28 |
| *Myrsine australis* | 7 | 32 | 12 | 1 | | 52 |
| *Myrsine divaricata* | | | | | 7 | 7 |
| *Neomyrtus pedunculata* | | | | | 1 | 1 |
| *Nothofagus solandri*(nf) | | | | | 100 | 100 |
| *Parsonsia heterophylla*(nf) | 72 | 45 | | 70 | 44 | 231 |
| *Pennantia corymbosa* | 17 | 21 | | 6 | | 44 |
| *Pittosporum tenuifolium* | | | 4 | 15 | 7 | 26 |
| *Podocarpus totara* | 8 | | | | | 8 |
| *Prumnopitys taxifolia* | | 1 | | | 4 | 5 |
| *Pseudopanax arboreus* | | 68 | 152 | | 5 | 225 |
| *Pseudopanax crassifolius* | 1 | 2 | | | 56 | 59 |
| *Pseudowintera colorata* | | | | | 2 | 2 |
| *Rubus cissoides* | | | | | 2 | 2 |
| *Rubus schmidelioides* | 7 | 2 | | | | 9 |
| *Sophora microphylla*(nf) | | 5 | | 6 | | 11 |
| Unknown | | 1 | | | | 1 |
| *Crataegus monogyna** | 1 | | | 1 | 8 | 10 |
| *Cytisus scoparium** (nf) | 1 | | 20 | | 2 | 23 |
| *Pinus radiata* (nf)* | | | | 1 | | 1 |
| *Prunus cerasifera** | | | | 1 | | 1 |
| *Rosa rubiginosa** | | | | 1 | | 1 |
| *Rubus fruticosus** | | | | 1 | 4 | 5 |
| *Teline monspessulana* (nf)* | | | | 24 | | 24 |
| MEAN SEEDLINGS/PLOT | 3.36 | 5.90 | 4.78 | 4.12 | 10.24 | |
| MEAN FF SEEDLINGS/PLOT | 1.88 | 4.72 | 4.24 | 2.02 | 6.8 | |

* = exotic species. (nf) = species with non-fleshy fruits. FF = fleshy-fruited.

One way ANOVA results show that show that there was a significant effect of site on mean seedlings per plot (df = 4, 236, F = 5.64, p = <0.001). Post hoc comparisons using the Tukey HSD test indicated that Taylors Bush had significantly higher mean seedlings per plot than Blythe Downs (P= <0.001), Lindon Lea (p = 0.001) and Kainsdale (p = 0.006).The difference between Taylors Bush and Glenkens was just non-significant (p = 0.051). The mean seedlings per plot of all other sites were statistically similar (Fig. 4.1)

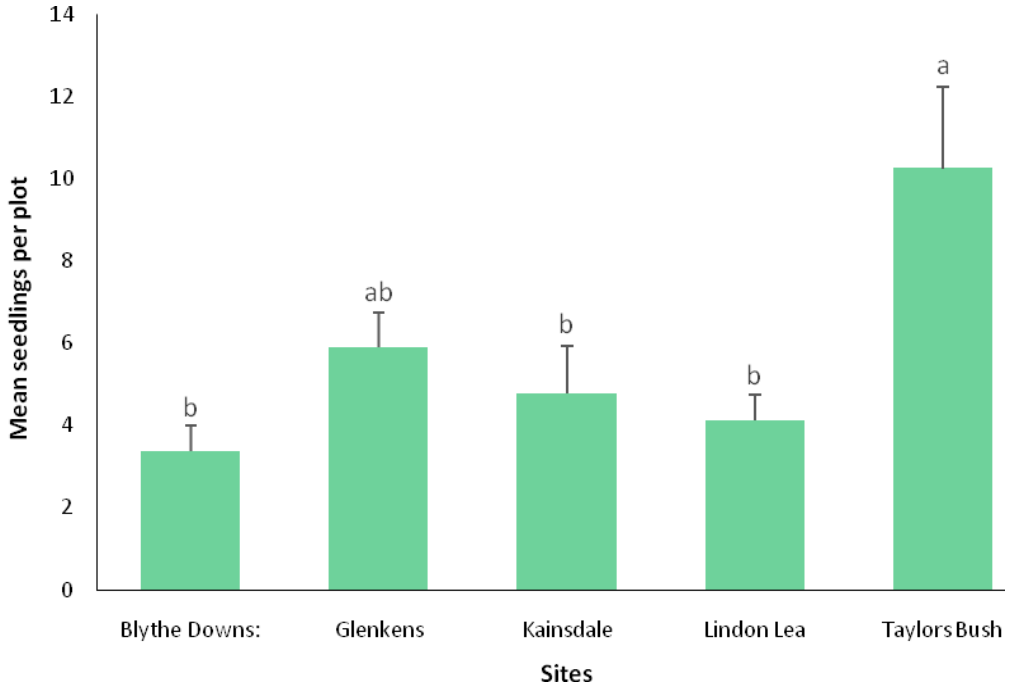


Figure 4.1 Mean seedlings per 0.5 x 0.5 m plot by site. Means sharing a letter were not significantly different according to Tukeys post hoc means test.

When only fleshy-fruited seedlings were included there was again a significant effect of site on mean seedlings per plot (df = 4, 235, F = 4.806, p = <0.001). Tukeys test showed that Taylors Bush had significantly higher fleshy-fruited seedlings per plot than Blythe Downs (p = 0.002) and Lindon Lea (p = 0.003) but that there were no other significant differences between sites (Fig. 4.2).

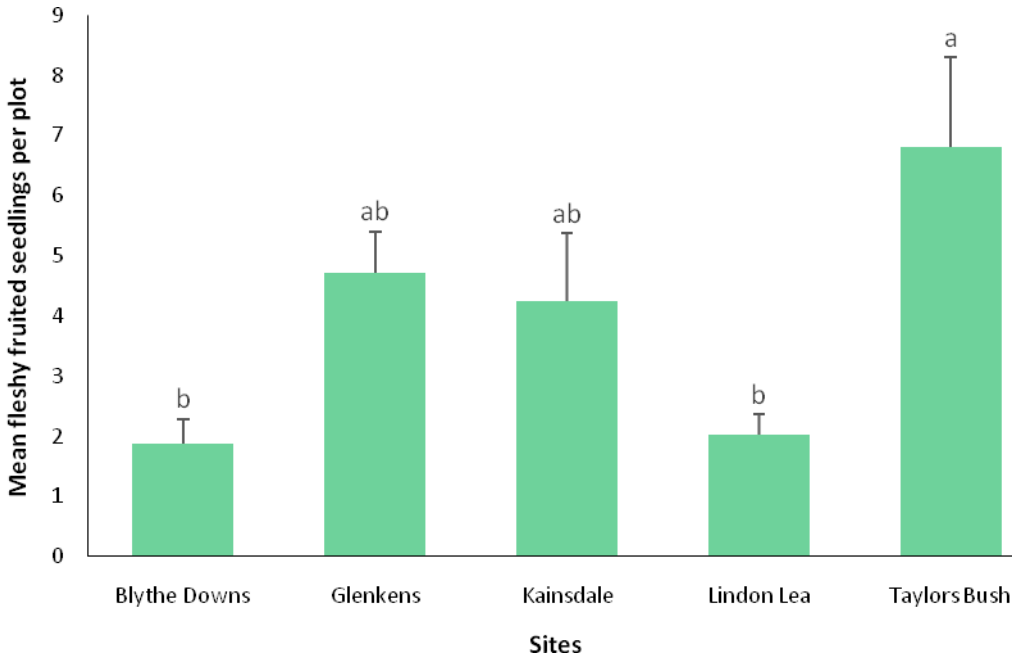


Figure 4.2 Mean fleshy-fruited seedlings per 0.5 x 0.5 m plot by site. Means sharing a letter were not significantly different according to Tukeys post hoc means test.

The linear regression results showed that mean number of fleshy-fruited seedlings was not significantly dependent on the mean number of frugivorous birds per 5 minute bird count ($F = 2.08$, $df = 4$, $p = 0.24$) although there was a weak trend.

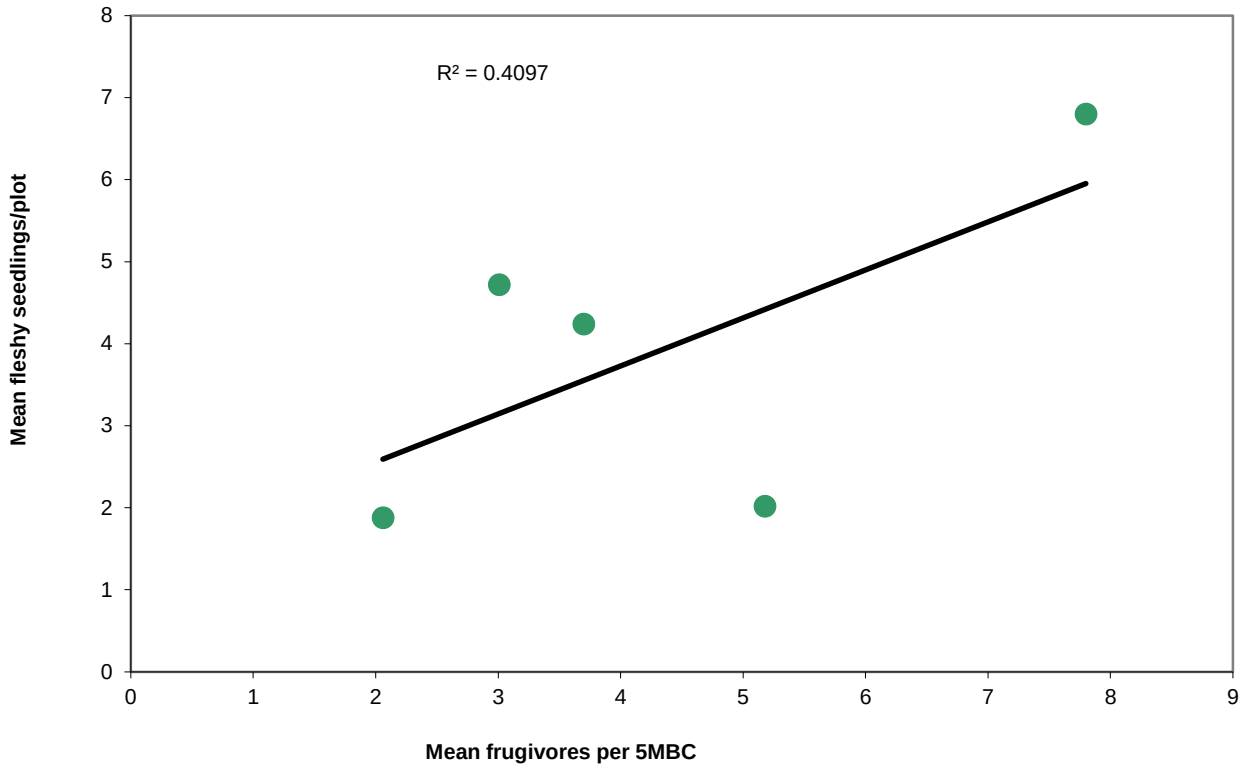


**Figure 4.3** Linear regression of fleshy-fruited seedlings by mean number of frugivorous birds per 5 minute bird count. (p = >0.05).

There was no evidence that the mean number of frugivorous birds was a significant predictor of the proportion of fleshy-fruited seedlings per plot (F=0.114, df = 4, p = 0.76) (Fig. 4.4).

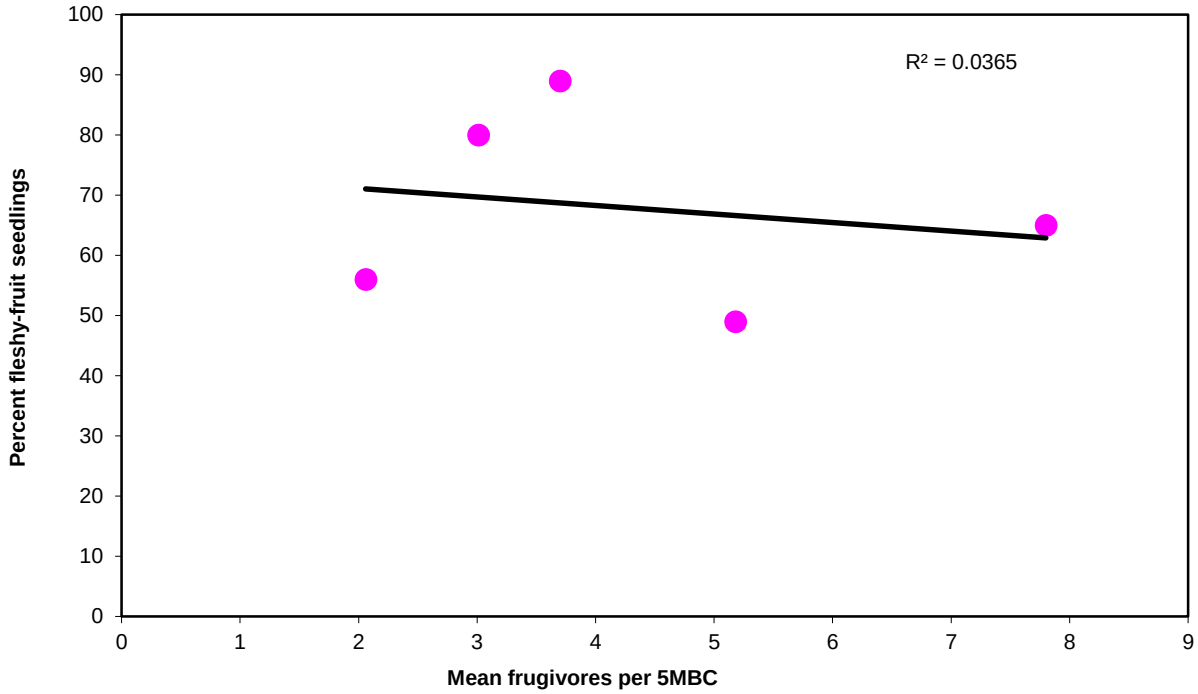


Figure 4.4 Proportion of fleshy-fruited seedlings per plot by mean frugivorous birds per 5 minute bird count. (p = 0.76).

Table 4.2 Comparisons of species richness and proportion of fleshy-fruited species between the latest vegetation surveys and the seedling plots; fragment sizes, mean birds per 5 minute count and percentage of birds that were exotic.

| | **Site area (ha)** | **Species richness** | | **% Fleshy-fruited species** | | **Mean birds/5MBC** | **% birds that were exotic** |
|---|---|---|---|---|---|---|---|
| | | Veg. survey | Seedlings | Veg. survey | Seedlings | | |
| Blythe Downs | 4 | 38 | 12 | 71 | 56 | 5.2 | 54 |
| Glenkens | 24 | 68 | 23 | 66 | 80 | 6.3 | 12 |
| Kainsdale | 2 | 44 | 15 | 73 | 89 | 6.4 | 37 |
| Lindon Lea | 10 | 72 | 21 | 65 | 49 | 7.5 | 25 |
| Taylors Bush | 8 | 58 | 25 | 83 | 65 | 10.6 | 26 |

## 4.4 Discussion

### 4.4.1 Long Distance Dispersal:

There were no species found in the covenants as seedlings that were not already listed as present in the sites at the last vegetation survey (conducted between 2003-2015). This means that seeds of species from other patches of native forest were not detected in the fragments; however we have no way of knowing whether seedlings found in the study were from seeds of plants within the covenant or from elsewhere. The lack of novel species was not unexpected considering the fragments are all fairly isolated from other patches of forest. Kereru (*Hemiphaga novaeseelandiae*) however, one of the key agents of long distance dispersal in New Zealand (Wotton and Kelly 2012), is capable of flying long distances and has the potential to bring seeds in from other patches of native forest or from food resources in the matrix. We observed a large influx of kereru at Blythe Downs when the totara (*Podocarpus totara*) trees came into fruit and their numbers went from very low during the majority of the study to high during fruiting. This suggests that they are spending their time elsewhere during other parts of the year when food at this site is sparse. Silvereyes (*Zosterops lateralis*), an important disperser, may not fly as far but are very capable of using the matrix and may bring in seeds from gardens or hedgerows or even other patches of forest if there are enough resources in between (Williams and Karl 1996, Kelly et al. 2006). Bellbirds (*Anthornis melanura)* are more selective frugivores than silvereyes and rely strongly on native fruit (Williams and Karl 1996) however they will leave forest provided there is a reliable food source nearby (Clout and Gaze 1984). The introduced blackbirds (*Turdus merula*) and thrushes (*Turdus philomelos*) are strong fliers and very comfortable with the matrix however they are potentially more likely to be bringing introduced plant species into the covenant than dispersing native plants (Buckley et al. 2006, Kelly et al. 2006, MacFarlane et al. 2016).

### 4.4.2 Plant diversity and variation between sites:

Seedling species richness was a lot lower in the seedling plots than in the lists of species that were recorded as present in the sites at the last survey, however this is expected as the majority of plant species found in the vegetation surveys were listed as rare or occasional.

The seedling plots at Taylors Bush had the highest species richness despite the fact that that there were ten fewer plots at this site. The is likely to be for similar reasons as the high abundances of seedlings, such as climate, time since fencing and high numbers of frugivorous birds. The two sites that are the smallest and have the highest edge to interior ratio (Blythe Downs and Kainsdale) are the two with the lowest species richness found in both the seedling plots and in their vegetation lists. While the largest site (Glenkens) did not have the highest species richness it was a close second to Taylors Bush in seedling richness, and to Lindon Lea in adult species richness at the last survey. These results would appear to at least partially support the common theory that larger fragments often bear more resemblance to continuous forest than do small fragments in terms of forest composition (Turner 1996, Cordeiro and Howe 2001).

While no novel species were found in the fragments there is some evidence of some potential small changes in composition. For example, *Coprosma propinqua* was the second most commonly found seedling species at Blythe Downs while it was only listed in the adult species list from 2007 as occasional. This suggests that it is being effectively dispersed by birds. As mentioned above the seedlings at Glenkens showed a higher number of fleshy fruited species than what would be expected from the last vegetation survey (2003). At Lindon Lea manuka (*Leptospermum scoparium)* and kanuka (*Kunzea ericoides*) are abundant in the canopy while no seedlings of these species were found in the plots however this is likely to be because these are early successional species which don't germinate well in shade (Grant 1967).

### 4.4.3 Seedling abundances:

Taylors Bush had the highest number of seedlings per plot by a significant margin with a mean of over ten seedlings per plot while the next highest mean was only 5.9. This corresponds with the fact that this fragment also had the highest mean number of frugivorous birds. There are, however other attributes of this fragment that have the potential to be contributing to the high seedling abundance. This covenant is further inland than the other covenants and has a wetter climate with a higher annual rainfall. The climate difference was especially pronounced in the year of this study as the Hurunui District in which the other covenants are

located experienced a major drought whereas this covenant was not in the affected area. The site is also the only site dominated by black beech which produces many seeds.

The second highest seedling abundance was found at Glenkens which was significantly higher than Lindon Lea and Blythe Downs. This is the largest of the five sites (24 ha with the others all <11 ha), which could be a contributing factor to the relatively high seedling abundance. Fragment size in general however, does not appear to be a determining factor in seedling abundance as the smallest covenant (Kainsdale) at 2.1 ha fell in the middle for seedling abundance and the site with the highest abundance was modest in size (8.3 ha). There were considerable signs of deer damage at Glenkens, however it has been found in the past that red deer (*Cervus elaphas*) generally eat at head height rather than lowering their head to eat small seedlings (Sweetapple and Nugent 2004). Deer sign was almost exclusively stripped bark of mature five-finger trees which fits with this theory. There were also occasional signs of pig (*Sus scrofus*) rooting but this was usually out in the open areas rather than in the forest interior. For these reasons, along with the fact that seedling abundance was high in this site it seems unlikely that either deer or pigs were having much of an effect on seedling mortality.

Lindon Lea had a high number of seed dispersing birds however it was the second lowest in terms of seedling abundance. This is likely due to the fact that until May 2015 cattle were grazing within the covenant and the fragment is still in the very early stages of recovery. There has been a visible increase in seedlings since fencing however and this was especially evident after rain in September 2015. Interestingly there were no five-finger seedlings found in this site despite them being common in the canopy and listed as frequent in the vegetation survey. Research has shown that five-finger is an especially palatable species for cattle (Walton et al. 1972, Timmins 2002). As this site was so recently grazed this seems a likely explanation for the abundance of adults and lack of seedlings.

The lowest seedling abundance was found at Blythe Downs, which fits with the fact that this site also had the lowest frugivorous birds. This fragment is very narrow and while no quadrats were placed in the stream area itself, a large proportion of this covenant is made up of the rocky banks of the gullies rather than deep soil and this may also have been a contributing factor in the comparatively low mean numbers of seedlings per plot. The eventual spring rain at this site occurred midway through the seedling study with the last third of the plots being

undertaken post rain. There was a very noticeable increase in seedlings after the rain, especially of totara, the fruiting of which coincided with the break of the drought. There were clusters of totara seedlings observed frequently on the last day of the study as well as a high number of kereru feeding on the totara fruit.

These results imply that the amount of time since fencing and rainfall level appear to be the major factors influencing overall seedling abundance in these fragments. The wettest fragment had the highest seedling abundance, while the most recently fenced fragment had the lowest. We observed an emergence of seedlings after the rain the late spring and early summer of 2015/16. The size of the fragment did not have any clear effect on seedling abundance.

### 4.4.4 Fleshy fruited seedlings:

The mean fleshy-fruited seedlings per plot follow the same pattern as when all seedlings were considered, with Taylors Bush having the highest abundance and Blythe Downs having the lowest. The explanations for this are likely to be similar to the reasons proposed for overall seedling abundance. If proportion of seedlings that are fleshy-fruited is considered rather than mean abundance however, then some differences emerge. Kainsdale had the highest proportion of fleshy-fruited seedlings at 89%. This is likely to be strongly influenced by the fact that five-finger seedlings were exceedingly abundant at this site, making up 64% of the total seedlings found.

Glenkens was second for proportion of fleshy-fruited seedlings despite the fact that it had the second lowest number of frugivorous birds. This site also had five-finger as its most common seedling which again could be a potential factor in the high proportion of fleshy-fruited plants. Five-finger was not as abundant at this site as at Kainsdale however, making up only 23% of the total seedlings, which suggests that other factors may be contributing to the high proportion of fleshy-fruited seedlings. The large size of the fragment could be a factor however again there was no apparent relationship between fragment size and proportions of fleshy-fruited seedlings. Another potential explanation is that this site had exceptionally high

numbers of the largely insectivorous brown creeper (*Mohoua novaeseelandiae*) which do take some fruit (Renaud et al. 2003). I also observed a flock feeding on the fruit of *Pittosporum tenuifolium* during this study. Therefore the abundance of these birds at this site may mean that they are making a contribution to seed dispersal despite the fact that fruit is only a supplementary part of their usual diet.

Taylors Bush was in the middle for the proportion of fleshy-fruited seedlings despite very high frugivorous bird numbers. This is potentially because it was so much more botanically diverse and because black beech, which is wind-dispersed, was a dominant species. Blythe Downs and Lindon Lea had the lowest proportions of fleshy-fruited seedlings respectively. Lindon Lea was the only site to have a proportion of <50% fleshy-fruited seedlings with 49%. These were also the two sites that had that lowest overall seedling abundance. Both of the sites had the wind-dispersed New Zealand jasmine *Parsonsia heterophylla* as their most common seedling which is likely to be driving the lower proportion of fleshy-fruited seedlings. Blythe Downs also had the lowest mean number of frugivorous birds. The low number of frugivorous birds and the low proportion of fleshy-fruited seedlings fit together but it is not easy to determine cause and effect. Lower numbers of frugivorous birds are likely to mean lower dispersal potential of fleshy-fruited plants, but less fleshy-fruited plants also means less food to attract and sustain frugivorous birds. Lindon Lea had the lowest percentage of fleshy-fruited species present in the covenant according to the last vegetation survey so it is not surprising that a similar pattern emerged in the seedling plots at this site.

The abundance of fleshy-fruited seedlings was not significantly related to the mean number of frugivorous birds, but it has to be recognised that with only five reserves the power of this test is very low. There were some suggestive patterns in the data. Taylors Bush had both the highest mean number of frugivorous birds and the highest mean number of fleshy-fruited seedlings, and Blythe Downs had the lowest frugivorous birds and lowest fleshy-fruited seedlings. Only a survey over a larger number of reserves could determine whether there is any statistical link between these variables.

The proportions of fleshy-fruited seedlings were not statistically dependent on frugivorous bird numbers at all. Nor do they appear to be affected by the size of the covenant with the

smallest fragment (Kainsdale) having the highest proportion of fleshy fruit. The variation among the sites appears to be the major factor influencing fleshy-fruited seed dispersal. Mean numbers of fleshy-fruited seedlings was determined by frugivorous bird numbers and also seemingly similar factors to overall abundance such as climate. The proportions of fleshy-fruited seedlings were likely influenced by the composition of the adult species present in the fragment. For example, most sites had a similar proportion of seedling species that produce fleshy fruit as the proportion of adult species present that produce fleshy fruit. The exception to this was Glenkens where only 66% of adult species were producers of fleshy fruit whereas 83% of the seedling species found were fleshy-fruited, which could imply that bird-mediated seed dispersal is becoming more successful in this site. Also, the two sites dominated by the wind-dispersed *Parsonsia heterophylla* had lower proportions of fleshy-fruited seedlings and the site that was dominated by five-finger had a high proportion of fleshy-fruited seedlings. The differences in bird composition may also be making a difference as some birds that aren't generally regarded as frugivorous such as brown creepers, grey warblers and finches may be making a contribution to seed dispersal of fleshy fruits (Renaud et al. 2003), especially where they occur in high numbers.

### 4.4.5 Exotic weeds:

Exotic plants made up only seven of the 51 species found over all sites. Four of these are bird-dispersed species. Two types of broom (*Cytisus scoparius* and *Teline monspessulana)* were found in relatively high numbers in Kainsdale and Lindon Lea respectively. Neither of these species are bird-dispersed. Bird-dispersed blackberry (*Rubus fruticosus)* and hawthorn (*Crataegus monogyna*) were present in reasonable numbers at Taylors Bush. The other three exotic species were only found once or twice over the whole study.

The relatively high incidence of broom at Kainsdale could potentially be explained by the fact that broom is a good coloniser that grows well in high light conditions. As this covenant is very small (2.1 ha) it has a high edge to interior ratio therefore plenty of opportunity for exotic plants such as this to gain a foothold. It does not do well in shady environments so with time as the canopy gradually becomes denser the species should decline.

Lindon Lea has only just been retired from grazing so pioneer species such as *Teline monspessulana* are likely to colonise at first, especially in open areas. A large digger track was made to assist in fence construction at this site at the beginning of the study. I observed after the rain that exotic weed species immediately colonised the track but that by the end of the study some natives such as five finger and wineberry (*Aristotelia serrata)* had taken hold underneath the weeds. *T. monspessulana* and blackberry were listed as abundant in the last vegetation survey. Only one blackberry seedling was found, however adult blackberry plants were observed commonly in the fragment.

The likely reason for the bird-dispersed weeds at Taylors Bush is that this site has been extensively wind and snow damaged with considerable tree-fall leaving numerous gaps in the otherwise dense canopy. When this is coupled with the high frugivorous bird numbers it seems likely that the birds are eating the blackberry and hawthorn and depositing the seeds throughout the site, and when they happen to fall in a gap they thrive. This phenomenon was very evident observationally at this site. For example one of the counting stations was set up next to the gap left by a very recently fallen tree. The ground in this gap was comparatively clear at the commencement of the study yet over the course of the year became thick with blackberry. Despite high plant diversity and the dense canopy the severe wind-fall damage and high bird numbers have the potential to facilitate the spread of hawthorn and especially blackberry in this site.

Interestingly, at Glenkens, no seedlings of exotic plant species were found at all. This corresponds with the fact that the proportion of exotic birds at this site was extremely low in comparison to all the other sites with only 12% of all birds observed being introduced. The site with the next lowest percentage of exotic birds (Lindon Lea) was double that at 24%. Several studies have shown that exotic birds in New Zealand, especially blackbirds and thrushes, are known as dispersers of exotic weed species (Buckley et al. 2006, MacFarlane et al. 2016) so their scarcity is likely to be an important factor in the lack of exotic plants. All exotic species listed as present at the last vegetation survey (2003) were listed as rare or occasional and our results suggest that this is still the case and this fragment is not at risk from invasive plants.

At Blythe Downs one broom (*Cytisus scoparius*) plant was the sole exotic seedling found. This is somewhat unexpected considering the site has a high edge to interior ratio and comparatively high numbers of introduced birds, however the exotic species that were listed as present in the last vegetation survey (2007) were all listed as rare or occasional so the seedling data seem to reflect that. Also only one bird-dispersed exotic species (hawthorn) is known to be present in the covenant so the higher numbers of exotic birds are not likely to be playing a major role in spreading weeds at this site.

Overall these results suggest that Glenkens and Blythe Downs are not at high risk of exotic weed invasions. Kainsdale and Lindon Lea are likely to be most affected by passively dispersed species, the risk of which should lessen with time. At Taylors Bush bird dispersed weed species are invading and the potential for further wind damage is a concern for weed spread. Barring more major tree-fall events however, the diversity of the site should enable native trees and shrubs to eventually shade out the blackberry and hawthorn.

### 4.4.6 Conclusion:

Variation in seedling densities was high between sites with seedling plots at Taylors Bush being significantly different from most of the other sites. The number and proportion of seedlings that are fleshy-fruited was not dependent on the mean number of frugivorous birds when using site means. The size of the sites does not appear to be affecting the seedling abundance but could play a part in species richness. Frugivorous birds are likely to be facilitating the spread of exotic weeds at Taylors Bush but this seems less likely in the other sites. In general fleshy-fruited native seedlings are common at the sites which suggests that bird-mediated seed dispersal is occurring adequately in these sites. This varies considerably however by site and has the potential to be influenced by frugivorous bird numbers, climate, time since fencing, edge to interior ratio and fragment size.

# Chapter 5: Overall discussion and conclusions

Forest fragmentation has been shown to have negative consequences for biodiversity around the world. These effects vary depending on spatial and temporal scale, geographic region and the suite of species in the affected landscape. Species are differentially resilient to the effects of fragmentation and thus ecosystem dynamics can be completely altered. Not only however, can the fragmentation of forest affect individual species but equally the essential mutualisms that the forest relies upon for regeneration such as seed dispersal.

The majority of the world's woody plant species rely on animals for dispersal (Carlo and Morales 2008) and a large proportion of these dispersers are birds. In New Zealand the forests having evolved without land mammals has meant that the unique avifauna is perhaps disproportionately important for forest regeneration, being responsible for much of New Zealand's woody plant seed dispersal and also making an important contribution to pollination (Kelly et al. 2010). As New Zealand's avifauna has suffered a large number of extinctions and severely reduced ranges since the arrival of humans and the mammalian predators that arrived with them (Holdaway 1989) there is potential for this, along with the ongoing effects of fragmentation and habitat loss in general to be resulting in reduced efficacy of seed dispersal of fleshy-fruited plants. There are two ways this could be occurring. Firstly by reducing the quantity of seed dispersal due to reduced disperser abundance and secondly by reduced dispersal quality due to less effective dispersers replacing those species which have been lost or reduced (Schupp 1993). This thesis looks at the former and aimed to establish how the bird seed dispersal mutualism is functioning in a severely fragmented part of the country with a potentially reduced suite of dispersers.

I based my study in five small, isolated forest fragments in North Canterbury. There were three ways in which I attempted to address the question. First I looked at whether the important seed dispersing birds were present in the fragments in sufficient numbers to disperse the seeds of the fleshy-fruited plant species (Chapter 2). I looked at the abundance and composition of the bird community to assess this. Secondly I looked at whether the fruit

was being removed from the trees (Chapter 3), and thirdly I assessed the seedling composition in the fragments to gain more of an idea of whether bird-dispersed species were regenerating successfully and being recruited into the forest ecosystem (Chapter 4).

The bird abundance study yielded some interesting insights into the avifauna of these small fragments. One of the most significant findings was that despite the fact that Canterbury is one of the most heavily deforested parts of the country and that all the fragments were isolated and surrounded by pasture, these small forest fragments still appear to be of high value. There were more birds in the fragments than expected and some had exceptionally high numbers for such small fragments. Stand outs were the very high numbers of bellbirds at the Lindon Lea covenant which were comparable to or even higher than some of the more biodiverse parts of the country, and the high number of brown creepers at Glenkens, which while not primarily frugivorous are one of the less common native bird species which a more restricted in range than some of the more tolerant native species. Importantly, four of the five primary frugivores (bellbird, silvereye, blackbird and thrush) were all present in all sites and the two natives (bellbird and silvereye) were among the most common birds at all sites. While not statistically a predictor, this ties in with the fact that *Coprosma robusta* fruit was almost all removed from monitored branches by the end of the season. Additionally, there were good numbers of fleshy-fruited seedlings in the fragments, as predicted by the number of frugivorous birds. In general these results suggest that seed dispersal may be functioning better in these fragments than would be expected given the fragmented landscape.

There are however some areas of potential concern. The other major finding from this study was that the five fragments were very different from one another in composition despite the sites being superficially similar in attributes in the same region. Each had its own distinctly different bird community. Bellbirds and/or silvereyes were among the most common birds at all sites but otherwise the compositions were very different. This suggests that there is a relatively low level of mixing between sites which has implications for conservation. Firstly it means that these fragments are especially important habitats for native birds and that despite their comparatively small size they provide important pockets of biodiversity. However, if they are isolated communities rather than a network of habitat among the landscape this can bring problems. Connectivity is important for maintaining bird populations longer term

especially when fragments are very small, and while many of the more common native birds found in the fragments are capable of utilising the matrix to some extent, there needs to be patches of food resources nearby.

An important function of seed dispersal in today's anthropogenically modified landscape is in the connecting of isolated patches and the restoring of ecologically degraded areas (Garcia et al. 2010). In New Zealand the kereru is probably the most important agent of long distance dispersal (Wotton and Kelly 2012), which is especially important in restoring connectivity. Kereru numbers in my study were not high (in contrast to bellbirds and silvereyes) although kereru were common at Blythe Downs especially when the totara were in fruit. They were occasional at Lindon Lea and low or absent in the other sites. This could suggest that long and medium distance dispersal is lacking in this area. This theory is backed up in the seedling chapter by the fact that no novel seedlings were found in the fragments suggesting that the seed dispersal occurring was mostly local, although I couldn't know the origin of the seedlings in my plots. Godoy and Jordano (2001) have developed a method of using DNA to track the parentage of seedlings which would add a lot to future seed dispersal studies. In some parts of New Zealand low kereru numbers would pose a second problem by also restricting the dispersal of large-seeded trees which are beyond the gape of most birds (Kelly et al. 2010), however in Canterbury this is not a problem as most fleshy fruited plants are small-seeded.

Introduced blackbirds and to a lesser extent thrushes were common in all sites. They are frugivorous and have been shown to contribute at varying levels to seed dispersal of native plants (Williams and Karl 1996, Kelly et al. 2006). They can also spread introduced weeds however (Buckley et al. 2006) and as they often spend more time in the matrix than the endemic frugivores and consume more adventive fruits this can facilitate weed invasions in the fragments (MacFarlane et al. 2016). Forest fragments are generally more vulnerable to weed invasions than continuous forest as edges can be entry points for these species that are often light loving. Introduced birds can deposit weed seeds at edges and in tree-fall gaps and exacerbate the problem (Richardson and Rejmánek 2011). There was evidence of this occurring at the Taylors Bush site where despite it being one of the most botanically diverse sites with the densest canopy, blackberry and hawthorn were encroaching into gaps left by extensive treefall damage.

There were some limitations to my study that could be improved upon for further research. The fruit removal study while still providing information about whether fruits were removed would have been far improved by a second tree species and by shorter intervals between branch monitoring. I carried out a large number of bird counts (463) which gave a comprehensive idea of bird composition and relative abundance however, the study was limited to one year and therefore could not account for inter-annual differences. Distance sampling could perhaps also be used in future to garner some numbers of birds per hectare. Also there were only five sites which limited the number of analyses that could be done. All of my sites were isolated and I used them as a setting for my study of seed dispersal in isolated fragments however it would be interesting to look further into the isolation factor and do some comparisons of bird and seedling compositions at varying levels of isolation, especially as my study has shown that these fragments appear to be distinct and somewhat separate communities.

This study has highlighted the importance of the forest fragments that remain and shown that perhaps especially in such a heavily modified area as Canterbury they can provide valuable havens of habitat for native species. It has also shown that even in such a degraded habitat, seed dispersal, on a local scale at least, still seems to be functioning sufficiently. It has identified that long distance dispersal among fragments and the restoration and reconnection that will come from it is a potential area for more research. Seed dispersal looks to be functioning better than expected currently and the future of seed dispersal in these fragments should be reasonably secure if medium and long-distance dispersal can be encouraged by actions such as the planting of native plants in the matrix that will provide food for kereru and the other more tolerant native species. The reintroduction of tui to Banks Peninsula recently, should it be successful, should restore another important facet of bird-mediated seed dispersal to Canterbury and as the second largest-bodied primary disperser also contribute to medium distance seed dispersal.

# References


Åberg, J., G. Jansson, J. E. Swenson, and P. Angelstam. 1995. The effect of matrix on the occurrence of hazel grouse (*Bonasa bonasia*) in isolated habitat fragments. Oecologia **103**:265-269.

Anderson, S. H., D. Kelly, J. J. Ladley, S. Molloy, and J. Terry. 2011. Cascading effects of bird functional extinction reduce pollination and plant density. Science **331**:1068-1071.

Anderson, S. H., D. Kelly, A. W. Robertson, J. J. Ladley, and J. G. Innes. 2006. S04-3 birds as pollinators and dispersers: a case study from New Zealand. Acta Zoologica Sinica **52**:112-115.

Andren, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos:355-366.

Arroyo-Rodríguez, V., A. Aguirre, J. Benítez-Malvido, and S. Mandujano. 2007. Impact of rain forest fragmentation on the population size of a structurally important palm species: *Astrocaryum mexicanum* at Los Tuxtlas, Mexico. Biological Conservation **138**:198-206.

Babweteera, F., P. Savill, and N. Brown. 2007. *Balanites wilsoniana*: regeneration with and without elephants. Biological Conservation **134**:40-47.

Bacles, C. F. E., A. J. Lowe, and R. A. Ennos. 2004. Genetic effects of chronic habitat fragmentation on tree species: the case of *Sorbus aucuparia* in a deforested Scottish landscape. Molecular Ecology **13**:573-584.

Báldi, A. 1996. Edge effects in tropical versus temperate forest bird communities: three alternative hypotheses for the explanation of differences. Acta Zoologica Academiae Scientarum Hungaricae **42**:163-172.

Barbaro, L., E. G. Brockerhoff, B. Giffard, and I. van Halder. 2012. Edge and area effects on avian assemblages and insectivory in fragmented native forests. Landscape Ecology **27**:1451-1463.

Bascompte, J., and P. Jordano. 2007. Plant-animal mutualistic networks: the architecture of biodiversity. Annual Review of Ecology, Evolution, and Systematics:567-593.

Bascompte, J., P. Jordano, and J. M. Olesen. 2006. Asymmetric coevolutionary networks facilitate biodiversity maintenance. Science **312**:431-433.

Bengtsson, J., P. Angelstam, T. Elmqvist, U. Emanuelsson, C. Folke, M. Ihse, F. Moberg, and M. Nyström. 2003. Reserves, resilience and dynamic landscapes. AMBIO: A Journal of the Human Environment **32**:389-396.

Benítez-Malvido, J., and M. Martínez-Ramos. 2003. Impact of forest fragmentation on understory plant species richness in Amazonia. Conservation biology **17**:389-400.

Bierregaard, R. O., and T. E. Lovejoy. 1989. Effects of forest fragmentation on Amazonian understory bird communities. Acta Amazonica **19**:215-241.

Boulton, R. L., Y. Richard, and D. P. Armstrong. 2008. Influence of food availability, predator density and forest fragmentation on nest survival of New Zealand robins. Biological Conservation **141**:580-589.

Bregman, T. P., C. H. Sekercioglu, and J. A. Tobias. 2014. Global patterns and predictors of bird species responses to forest fragmentation: Implications for ecosystem function and conservation. Biological Conservation **169**:372-383.

Brockerhoff, E. G., H. Jactel, J. A. Parrotta, C. P. Quine, and J. Sayer. 2008. Plantation forests and biodiversity: oxymoron or opportunity? Springer, Netherlands.

Brooks, T. M., R. A. Mittermeier, C. G. Mittermeier, G. A. Da Fonseca, A. B. Rylands, W. R. Konstant, P. Flick, J. Pilgrim, S. Oldfield, and G. Magin. 2002. Habitat loss and extinction in the hotspots of biodiversity. Conservation biology **16**:909-923.

Buckley, Y. M., S. Anderson, C. P. Catterall, R. T. Corlett, T. Engel, C. R. Gosper, R. Nathan, D. M. Richardson, M. Setter, and O. Spiegel. 2006. Management of plant invasions mediated by frugivore interactions. Journal of Applied Ecology **43**:848-857.

Burgess, V. J., D. Kelly, A. W. Robertson, and J. J. Ladley. 2006. Positive effects of forest edges on plant reproduction: literature review and a case study of bee visitation to flowers of Peraxilla tetrapetala (Loranthaceae). New Zealand journal of ecology:179-190.

Burkey, T. V. 1999. Extinction in fragmented habitats predicted from stochastic birth–death processes with density dependence. Journal of Theoretical Biology **199**:395-406.

Burns, B. R., C. G. Floyd, M. C. Smale, and G. Arnold. 2011. Effects of forest fragment management on vegetation condition and maintenance of canopy composition in a New Zealand pastoral landscape. Austral Ecology **36**:153-166.

Burns, K. C. 2012. Are introduced birds unimportant mutualists? A case study of frugivory in European blackbirds (*Turdus merula*). New Zealand Journal of Ecology **36**:171-176.

Burrows, C. 1995. Germination behaviour of the seeds of the New Zealand species Aristotelia serrata, Coprosma robusta, Cordyline australis, Myrtus obcordata, and Schefflera digitata. New Zealand journal of botany **33**:257-264.

Carlo, T. A., and J. M. Morales. 2008. Inequalities in fruit-removal and seed dispersal: consequences of bird behaviour, neighbourhood density and landscape aggregation. Journal of Ecology **96**:609-618.

Cassey, P. 2001. Determining variation in the success of New Zealand land birds. Global Ecology and Biogeography **10**:161-172.

Caves, E. M., S. B. Jennings, J. Hillerislambers, J. J. Tewksbury, and H. S. Rogers. 2013. Natural experiment demonstrates that bird loss leads to cessation of dispersal of native seeds from intact to degraded forests. PloS one **8**:e65618.

Clark, C. J., J. R. Poulsen, E. F. Connor, and V. T. Parker. 2004. Fruiting trees as dispersal foci in a semi-deciduous tropical forest. Oecologia **139**:66-75.

Clark, D. A., and D. B. Clark. 1984. Spacing dynamics of a tropical rain forest tree: evaluation of the Janzen-Connell model. The American Naturalist **124**:769-788.

Clout, M., P. Gaze, J. Hay, and B. Karl. 1986. Habitat use and spring movements of New Zealand pigeons at Lake Rotoroa, Nelson Lakes National park. Notornis **33**:37-44.

Clout, M. N., and P. D. Gaze. 1984. Effects of plantation forestry on birds in New Zealand. Journal of Applied Ecology **21**:795-815.

Clout, M. N., and J. R. Hay. 1989. The importance of birds as browsers, pollinators and seed dispersers in New Zealand forests. New Zealand Journal of Ecology **12**:27-33.

Comita, L. S., S. A. Queenborough, S. J. Murphy, J. L. Eck, K. Xu, M. Krishnadas, N. Beckman, and Y. Zhu. 2014. Testing predictions of the Janzen–Connell hypothesis: a meta-analysis of experimental evidence for distance- and density-dependent seed and seedling survival. Journal of Ecology **102**:845-856.

Connell, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. Dynamics of Populations **298**:312.

Cordeiro, N. J., and H. F. Howe. 2001. Low recruitment of trees dispersed by animals in African forest fragments. Conservation biology **15**:1733-1741.

Cordeiro, N. J., and H. F. Howe. 2003. Forest fragmentation severs mutualism between seed dispersers and an endemic African tree. Proceedings of the National Academy of Sciences of the United States of America **100**:14052-14056.

Cowan, P. E. 1990. Fruits, seeds, and flowers in the diet of brushtail possums, *Trichosurus vulpecula*, in lowland podocarp/mixed hardwood forest, Orongorongo Valley, New Zealand. New Zealand Journal of Zoology **17**:549-566.

Cramer, J. M., R. C. G. Mesquita, and B. G. Williamson. 2007. Forest fragmentation differentially affects seed dispersal of large and small-seeded tropical trees. Biological Conservation **137**:415-423.

Dawson, D. G., and P. C. Bull. 1975. Counting birds in New Zealand forests. Notornis **22**:101-109.

Debinski, D. M., and R. D. Holt. 2000. A survey and overview of habitat fragmentation experiments. Conservation biology **14**:342-355.

Deconchat, M., E. G. Brockerhoff, and L. Barbaro. 2009. Effects of surrounding landscape composition on the conservation value of native and exotic habitats for native forest birds. Forest Ecology and Management **258**:S196-S204.

Denyer, K., B. Burns, and J. Ogden. 2006. Buffering of native forest edge microclimate by adjoining tree plantations. Austral Ecology **31**:478-489.

Diamond, J. M. 1984. Distributions of New Zealand birds on real and virtual islands. New Zealand Journal of Ecology **7**:37-55.

Diamond, J. M., K. D. Bishop, and S. v. Balen. 1987. Bird survival in an isolated Javan woodland: island or mirror? Conservation biology **1**:132-142.

Dowding, J. E., and E. C. Murphy. 2001. The impact of predation by introduced mammals on endemic shorebirds in New Zealand: a conservation perspective. Biological Conservation **99**:47-64.

Ewers, R. M., and R. K. Didham. 2006. Confounding factors in the detection of species responses to habitat fragmentation. Biological Reviews **81**:117-142.

Ewers, R. M., and R. K. Didham. 2007. The effect of fragment shape and species' sensitivity to habitat edges on animal population size. Conservation biology **21**:926-936.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. Annual review of ecology, evolution, and systematics **34**:487-515.

Farwig, N., and D. G. Berens. 2012. Imagine a world without seed dispersers: a review of threats, consequences and future directions. Basic and Applied Ecology **13**:109-115.

Federman, S., A. Dornburg, D. C. Daly, A. Downie, G. H. Perry, A. D. Yoder, E. J. Sargis, A. F. Richard, M. J. Donoghue, and A. L. Baden. 2016. Implications of lemuriform extinctions for the Malagasy flora. Proceedings of the National Academy of Sciences **113**:201523825.

Fine, P. V. A. 2002. The invasibility of tropical forests by exotic plants. Journal of Tropical Ecology **18**:687-705.

Galetti, M., C. P. Alves-Costa, and E. Cazetta. 2003. Effects of forest fragmentation, anthropogenic edges and fruit colour on the consumption of ornithocoric fruits. Biological Conservation **111**:269-273.

Galli, A. E., C. F. Leck, and R. T. Forman. 1976. Avian distribution patterns in forest islands of different sizes in central New Jersey. The Auk **99**:356-364.

Garcia, D., and N. P. Chacoff. 2007. Scale-dependent effects of habitat fragmentation on hawthorn pollination, frugivory, and seed predation. Conservation biology **21**:400-411.

Garcia, D., R. Zamora, and G. C. Amico. 2010. Birds as suppliers of seed dispersal in temperate ecosystems: conservation guidelines from real-world landscapes. Conservation biology **24**:1070-1079.

Gascon, C., T. E. Lovejoy, R. O. Bierregaard Jr, J. R. Malcolm, P. C. Stouffer, H. L. Vasconcelos, W. F. Laurance, B. Zimmerman, M. Tocher, and S. Borges. 1999. Matrix habitat and species richness in tropical forest remnants. Biological Conservation **91**:223-229.

Gascon, C., G. B. Williamson, and G. A. da Fonseca. 2000. Receding forest edges and vanishing reserves. Science **288**:1356-1358.

Ghiselin, J. 1977. Analyzing ecotones to predict biotic productivity. Environmental Management **1**:235-238.

Godoy, J. A., and P. Jordano. 2001. Seed dispersal by animals: exact identification of source trees with endocarp DNA microsatellites. Journal of Molecular Ecology.

Gorchov, D. L., F. Cornejo, C. Ascorra, and M. Jaramillo. 1993. The role of seed dispersal in the natural regeneration of rain forest after strip-cutting in the Peruvian Amazon. Vegetatio **107**:339-349.

Grant, D. 1967. Factors affecting the establishment of manuka (Leptospermum scoparium). Pages 129-134 *in* Proceedings 20th NZ Weed Pest Control Conf.

Haila, Y. 2002. A conceptual genealogy of fragmentation research: from island biogeography to landscape ecology. Ecological Applications **12**:321-334.

Hanski, I. 1999. Metapopulation ecology. Oxford University Press, Oxford, UL.

Harris, L. D. 1988. Edge effects and conservation of biotic diversity. Conservation biology **2**:330-332.

Henle, K., K. F. Davies, M. Kleyer, C. Margules, and J. Settele. 2004. Predictors of species sensitivity to fragmentation. Biodiversity & Conservation **13**:207-251.

Herrera, C. M. 2002. Seed dispersal by vertebrates. Pages 185-208 *in* C. M. Herrera and O. Pellmyr, editors. Plant–animal interactions: an evolutionary approach. Oxford, UK, Blackwell Science.

Herrera, J., and D. Garcia. 2010. Effects of forest fragmentation on seed dispersal and seedling establishment in ornithochorous trees. Conservation biology **24**:1089-1098.

Hill, J. L., and P. J. Curran. 2003. Area, shape and isolation of tropical forest fragments: effects on tree species diversity and implications for conservation. Journal of Biogeography **30**:1391-1403.

Holdaway, R. N. 1989. New Zealand's pre-human avifauna and its vulnerability. New Zealand Journal of Ecology **12**:11-25.

Howe, H. F. 1993. Specialized and generalized dispersal systems: where does 'the paradigm' stand? Vegetatio **107**:3-13.

Howe, H. F., and M. N. Miriti. 2004. When seed dispersal matters. BioScience **54**:651-660.

Howe, H. F., and J. Smallwood. 1982. Ecology of seed dispersal. Annual Review of Ecology and Systematics **13**:201-228.

Innes, J., D. Kelly, J. M. Overton, and C. Gillies. 2010. Predation and other factors currently limiting New Zealand forest birds. New Zealand Journal of Ecology **34**:86-114.

Jana, R. C. 2012. Animal seed dispersal and its consequences for plant recruitment. . PhD thesis. University of Canterbury, New Zealand.

Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. The American Naturalist **104**:501-528.

Jordano, P., C. García, J. A. Godoy, and J. L. García-Castaño. 2007. Differential contribution of frugivores to complex seed dispersal patterns. Proceedings of the National Academy of Sciences **104**:3278-3282.

Kawakami, K., L. Mizusawa, and H. Higuchi. 2009. Re-established mutualism in a seed-dispersal system consisting of native and introduced birds and plants on the Bonin Islands, Japan. Ecological Research **24**:741-748.

Kelly, D., J. Ladley, A. W. Robertson, and D. Norton. 2000. Limited forest fragmentation improves reproduction in the declining New Zealand mistletoe Peraxilla tetrapetala (Loranthaceae). CONSERVATION BIOLOGY SERIES-CAMBRIDGE-:241-252.

Kelly, D., J. J. Ladley, and A. W. Robertson. 2007. Is the pollen-limited mistletoe *Peraxilla tetrapetala* (Loranthaceae) also seed limited? Austral Ecology **32**:850-857.

Kelly, D., J. J. Ladley, A. W. Robertson, S. H. Anderson, D. M. Wotton, and S. K. Wiser. 2010. Mutualisms with the wreckage of an avifauna: the status of bird pollination and fruit-dispersal in New Zealand. New Zealand Journal of Ecology **34**:66.

Kelly, D., A. W. Robertson, J. J. Ladley, S. H. Anderson, and R. J. McKenzie. 2006. Relative (un) importance of introduced animals as pollinators and dispersers of native plants. Pages 227-245 *in* R. B. Allen and W. G. Lee, editors. Biological invasions in New Zealand. Springer, Berlin, Germany.

Kirika, J. M., B. Bleher, K. Bohning-Gaese, R. Chira, and N. Farwig. 2008. Fragmentation and local disturbance of forests reduce frugivore diversity and fruit removal in *Ficus thonningii* trees. Basic and Applied Ecology **9**:663-672.

Kupfer, J. A., G. P. Malanson, and S. B. Franklin. 2006. Not seeing the ocean for the islands: the mediating influence of matrix-based processes on forest fragmentation effects. Global Ecology and Biogeography **15**:8-20.

Laurance, W. F. 2005. When bigger is better: the need for Amazonian mega-reserves. Trends in Ecology & Evolution **20**:645-648.

Laurance, W. F., and R. O. Bierregaard. 1997. Tropical forest remnants: ecology, management, and conservation of fragmented communities. University of Chicago Press, Chicago, USA.

Laurance, W. F., P. Delamônica, S. G. Laurance, H. L. Vasconcelos, and T. E. Lovejoy. 2000. Conservation: rainforest fragmentation kills big trees. Nature **404**:836-836.

Laurance, W. F., L. V. Ferreira, J. M. Rankin-de Merona, and S. G. Laurance. 1998. Rain forest fragmentation and the dynamics of Amazonian tree communities. Ecology **79**:2032-2040.

Laurance, W. F., T. E. Lovejoy, H. L. Vasconcelos, E. M. Bruna, R. K. Didham, P. C. Stouffer, C. Gascon, R. O. Bierregaard, S. G. Laurance, and E. Sampaio. 2002. Ecosystem decay of Amazonian forest fragments: a 22-year investigation. Conservation biology **16**:605-618.

Lehouck, V., T. Spanhove, S. Demeter, N. Groot, and L. Lens. 2009. Complementary seed dispersal by three avian frugivores in a fragmented Afromontane forest. Journal of Vegetation Science **20**:1110-1120.

Lenth, R. V. 2016. Least-Squares Means: The R Package lsmeans. Journal of Statistical Software **69**:1-33.

Levey, D. J. 1988. Tropical wet forest treefall gaps and distributions of understory birds and plants. Ecology **69**:1076-1089.

Levins, R., and M. G. Extinction. 1970. Some mathematical problems in biology. American Mathematical Society, Providence, RI, USA.

Lindell, C. A., S. K. Riffell, S. A. Kaiser, A. L. Battin, M. L. Smith, and T. D. Sisk. 2007. Edge responses of tropical and temperate birds. The Wilson Journal of Ornithology **119**:205-220.

Lindenmayer, D. B., and J. F. Franklin. 2002. Conserving forest biodiversity: a comprehensive multiscaled approach. Island Press, Washington, USA.

Lord, J. M., A. S. Markey, and J. Marshall. 2002. Have frugivores influenced the evolution of fruit traits in New Zealand. Pages 55-68 *in* D. J. Levey, W. R. Silva, and M. Galetti, editors. Seed dispersal and frugivory: ecology, evolution and conservation. . CABI Publishing, Wallingford, UK.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. . Princeton University Press, Princeton, NJ, USA.

MacFarlane, A. E., D. Kelly, and J. V. Briskie. 2016. Introduced blackbirds and song thrushes: useful substitutes for lost mid-sized native frugivores, or weed vectors? New Zealand Journal of Ecology **40**:0-0.

Magnago, L. F. S., D. P. Edwards, F. A. Edwards, A. Magrach, S. V. Martins, and W. F. Laurance. 2014. Functional attributes change but functional richness is unchanged after fragmentation of Brazilian Atlantic forests. Journal of Ecology **102**:475-485.

Malmborg, P. K., and M. F. Willson. 1988. Foraging ecology of avian frugivores and some consequences for seed dispersal in an Illinois woodlot. The Condor **90**:173-186.

Mander, C. J., J. R. Hay, and R. Powlesland. 1998. Monitoring and management of kereru (*Hemiphaga novaeseelandiae*). 047821751X, Department of Conservation Wellington, New Zealand.

Markl, J. S., M. Schleuning, P. M. Forget, P. Jordano, J. E. Lambert, A. Traveset, S. J. Wright, and K. Böhning-Gaese. 2012. Meta-Analysis of the Effects of Human Disturbance on Seed Dispersal by Animals. Conservation biology **26**:1072-1081.

Martin, P. H., and C. D. Canham. 2010. Dispersal and recruitment limitation in native versus exotic tree species: life-history strategies and Janzen-Connell effects. Oikos **119**:807-824.

Matlack, G. R. 1993. Microenvironment variation within and among forest edge sites in the eastern United States. Biological Conservation **66**:185-194.

Matlack, G. R. 1994. Vegetation dynamics of the forest edge-trends in space and successional time. Journal of Ecology **82**:113-123.

McDiarmid, R. W., R. E. Ricklefs, and M. S. Foster. 1977. Dispersal of *Stemmadenia donnell-smithii* (Apocynaceae) by birds. Biotropica **9**:9-25.

McEuen, A. B., and L. M. Curran. 2004. Seed dispersal and recruitment limitation across spatial scales in temperate forest fragments. Ecology **85**:507-518.

McGlone, M. S., S. J. Richardson, and G. J. Jordan. 2010. Comparative biogeography of New Zealand trees: species richness, height, leaf traits and range sizes. New Zealand Journal of Ecology **34**:137.

McIntyre, S., and R. Hobbs. 1999. A framework for conceptualizing human effects on landscapes and its relevance to management and research models. Conservation biology **13**:1282-1292.

Meehan, H. J., K. R. McConkey, and D. R. Drake. 2002. Potential disruptions to seed dispersal mutualisms in Tonga, Western Polynesia. Journal of Biogeography **29**:695-712.

Moran, C., C. Catterall, R. J. Green, and M. F. Olsen. 2004. Functional variation among frugivorous birds: implications for rainforest seed dispersal in a fragmented subtropical landscape. Oecologia **141**:584-595.

Mühlenberg, M., T. Hovestadt, and J. Röser. 1991. Are There Minimal Areas for Animal Populations? Pages 227-264 *in* A. Seitz and V. Loeschcke, editors. Species Conservation: A Population-Biological Approach. Springer, Berlin, Germany.

Murcia, C. 1996. Forest fragmentation and the pollination of neotropical plants. Pages 19-33 *in* J. Schelhas and R. S. Greenberg, editors. Forest Patches in Tropical Landscapes. Island Press, London, UK.

Murphy, D. J., and D. Kelly. 2001. Scarce or distracted? Bellbird (Anthornis melanura) foraging and diet in an area of inadequate mistletoe pollination. New Zealand Journal of Ecology:69-81.

Nathan, R., and H. C. Muller-Landau. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. Trends in Ecology & Evolution **15**:278-285.

Ne'eman, G., and I. Izhaki. 1996. Colonization in an abandoned East-Mediterranean vineyard. Journal of Vegetation Science **7**:465-472.

Norton, D. A. 2002. Edge effects in a lowland temperate New Zealand rainforest. Department of Conservation, Wellington, New Zealand.

O'Donnell, C. F., and P. J. Dilks. 1994. Foods and foraging of forest birds in temperate rainforest, South Westland, New Zealand. New Zealand Journal of Ecology **18**:87-107.

Packer, A., and K. Clay. 2000. Soil pathogens and spatial patterns of seedling mortality in a temperate tree. Nature **404**:278-281.

Paton, P. W. 1994. The effect of edge on avian nest success: how strong is the evidence? Conservation biology **8**:17-26.

Pejchar, L., R. M. Pringle, J. Ranganathan, J. R. Zook, G. Duran, F. Oviedo, and G. C. Daily. 2008. Birds as agents of seed dispersal in a human-dominated landscape in southern Costa Rica. Biological Conservation **141**:536-544.

Peters, H. A. 2003. Neighbour-regulated mortality: the influence of positive and negative density dependence on tree populations in species-rich tropical forests. Ecology Letters **6**:757-765.

Reid, N. 1991. Coevolution of mistletoes and frugivorous birds?*. Australian journal of ecology **16**:457-469.

Renaud, P., H. Verheyden-Tixier, and B. Dumont. 2003. Damage to saplings by red deer (Cervus elaphus): effect of foliage height and structure. Forest Ecology and Management **181**:31-37.

Restrepo, C., N. Gomez, and S. Heredia. 1999. Anthropogenic edges, treefall gaps, and fruit-frugivore interactions in a neotropical montane forest. Ecology **80**:668-685.

Richardson, D. M., and M. Rejmánek. 2011. Trees and shrubs as invasive alien species–a global review. Diversity & Distributions **17**:788-809.

Robertson, A. W., A. Trass, J. J. Ladley, and D. Kelly. 2006. Assessing the benefits of frugivory for seed germination: the importance of the deinhibition effect. Functional Ecology **20**:58-66.

Robinson, S. K. 1998. Another threat posed by forest fragmentation: reduced food supply. The Auk **115**:1-3.

Sanders, M. D., and R. F. Maloney. 2002. Causes of mortality at nests of ground-nesting birds in the Upper Waitaki Basin, South Island, New Zealand: a 5-year video study. Biological Conservation **106**:225-236.

Santos, T., and J. Tellería. 1994. Influence of forest fragmentation on seed consumption and dispersal of Spanish juniper *Juniperus thurifera*. Biological Conservation **70**:129-134.

Saunders, A., and D. A. Norton. 2001. Ecological restoration at mainland islands in New Zealand. Biological Conservation **99**:109-119.

Saunders, D. A., R. J. Hobbs, and C. R. Margules. 1991. Biological consequences of ecosystem fragmentation: a review. Conservation biology **5**:18-32.

Scariot, A. 1999. Forest fragmentation effects on palm diversity in central Amazonia. Journal of Ecology **87**:66-76.

Schmechel, F. 2009. Bird monitoring on Banks Peninsula.

Schupp, E. W. 1993. Quantity, quality and the effectiveness of seed dispersal by animals. Pages 15-29 *in* T. H. Fleming and A. Estrada, editors. Frugivory and seed dispersal: ecological and evolutionary aspects. Springer, New York, NY, USA.

Schupp, E. W., and M. Fuentes. 1995. Spatial patterns of seed dispersal and the unification of plant population ecology. Ecoscience **2**:267-275.

Sekercioglu, C. H. 2006. Increasing awareness of avian ecological function. Trends in Ecology & Evolution **21**:464-471.

Sekercioglu, C. H., and N. S. Sodhi. 2007. Conservation Biology: predicting birds' responses to forest fragmentation. Current Biology **17**:R838-R840.

Silander, J. A. 1978. Density-dependent control of reproductive success in Cassia biflora. Biotropica **10**:292-296.

Sisk, T. D., and J. Battin. 2002. Habitat edges and avian ecology: geographic patterns and insights for western landscapes. Studies in Avian Biology **25**:30-48.

Snow, D. W. 1971. Evolutionary aspects of fruit-eating by birds. Ibis **113**:194-202.

Spiegel, O., and R. Nathan. 2007. Incorporating dispersal distance into the disperser effectiveness framework: frugivorous birds provide complementary dispersal to plants in a patchy environment. Ecology Letters **10**:718-728.

Spurr, E. B., B. Warburton, and K. W. Drew. 1992. Bird abundance in different-aged stands of rimu (*Dacrydium cupressinum*)-implications for coupe-logging. New Zealand Journal of Ecology **16**:109-118.

Stephens, S. E., D. N. Koons, J. J. Rotella, and D. W. Willey. 2004. Effects of habitat fragmentation on avian nesting success: a review of the evidence at multiple spatial scales. Biological Conservation **115**:101-110.

Stiles, E. W. 1993. The influence of pulp lipids on fruit preference by birds. Vegetatio **107**:227-235.

Stouffer, P. C., R. O. Bierregaard, C. Strong, and T. E. Lovejoy. 2006. Long-Term Landscape Change and Bird Abundance in Amazonian Rainforest Fragments. Conservation biology **20**:1212-1223.

Sweetapple, P. J., and G. Nugent. 2004. Seedling ratios: a simple method for assessing ungulate impacts on forest understories. Wildlife Society Bulletin **32**:137-147.

T.E.R.R.A.I.N, T. E. R. R. A. a. I. N. 2015. *Coprosma robusta* (Karamu).

Tabarelli, M., W. Mantovani, and C. A. Peres. 1999. Effects of habitat fragmentation on plant guild structure in the montane Atlantic forest of southeastern Brazil. Biological Conservation **91**:119-127.

Terborgh, J., G. Nuñez-Iturri, N. C. Pitman, F. H. C. Valverde, P. Alvarez, V. Swamy, E. G. Pringle, and C. T. Paine. 2008. Tree recruitment in an empty forest. Ecology **89**:1757-1768.

Thompson, J. N., and M. F. Willson. 1978. Disturbance and the dispersal of fleshy fruits. Science **200**:1161-1163.

Tilman, D., R. M. May, C. L. Lehman, and M. A. Nowak. 1994. Habitat destruction and the extinction debt. Nature **371**:65-66.

Timmins, S. M. 2002. Impact of cattle on conservation land licensed for grazing in South Westland, New Zealand. New Zealand Journal of Ecology **26**:107-120.

Trakhtenbrot, A., R. Nathan, G. Perry, and D. M. Richardson. 2005. The importance of long-distance dispersal in biodiversity conservation. Diversity & Distributions **11**:173-181.

Traveset, A., A. Robertson, and J. Rodríguez-Pérez. 2007. A review on the role of endozoochory on seed germination. Pages 78-103 *in* A. J. Dennis, editor. Seed dispersal: theory and its application in a changing world. CABI Publishing, Wallingford, UK.

Tscharntke, T., C. H. Sekercioglu, T. V. Dietsch, N. S. Sodhi, P. Hoehn, and J. M. Tylianakis. 2008. Landscape constraints on functional diversity of birds and insects in tropical agroecosystems. Ecology **89**:944-951.

Turner, I. 1996. Species loss in fragments of tropical rain forest: a review of the evidence. Journal of Applied Ecology **33**:200-209.

Uriarte, M., M. Anciães, M. T. Da Silva, P. Rubim, E. Johnson, and E. M. Bruna. 2011. Disentangling the drivers of reduced long-distance seed dispersal by birds in an experimentally fragmented landscape. Ecology **92**:924-937.

Walton, T., A. E. Beverage, and R. L. Knowles. 1972. Role of livestock in forest management. New Zealand Journal of Agriculture.

Watson, J. E., R. J. Whittaker, and T. P. Dawson. 2004. Habitat structure and proximity to forest edge affect the abundance and distribution of forest-dependent birds in tropical coastal forests of southeastern Madagascar. Biological Conservation **120**:311-327.

Wenny, D. G., and D. J. Levey. 1998. Directed seed dispersal by bellbirds in a tropical cloud forest. Proceedings of the National Academy of Sciences **95**:6204-6207.

Whelan, C. J., D. G. Wenny, and R. J. Marquis. 2008. Ecosystem services provided by birds. Annals of the New York Academy of Sciences **1134**:25-60.

Whitaker, A. H. 1987. The roles of lizards in New Zealand plant reproductive strategies. New Zealand journal of botany **25**:315-328.

Wilcove, D. S., C. H. McLellan, and A. P. Dobson. 1986. Habitat fragmentation in the temperate zone. Conservation biology **6**:237-256.

Wilcox, B. A., and D. D. Murphy. 1985. Conservation strategy: the effects of fragmentation on extinction. The American Naturalist **125**:879-887.

Williams, P. A., and B. J. Karl. 1996. Fleshy fruits of indigenous and adventive plants in the diet of birds in forest remnants, Nelson, New Zealand. New Zealand Journal of Ecology **20**:127-145.

Williams, P. A., B. J. Karl, P. Bannister, and W. G. Lee. 2000. Small mammals as potential seed dispersers in New Zealand. Austral Ecology **25**:523-532.

Willson, M. F., D. A. Graff, and C. J. Whelan. 1990. Color preferences of frugivorous birds in relation to the colors of fleshy fruits. Condor:545-555.

Willson, M. F., and A. Traveset. 2000. The ecology of seed dispersal. Pages 85-110 *in* M. Fenner, editor. Seeds: the ecology of regeneration in plant communities. CABI Publishing, Wallingford, UK.

Wotton, D. M., D. R. Drake, R. G. Powlesland, and J. J. Ladley. 2016. The role of lizards as seed dispersers in New Zealand. Journal of the Royal Society of New Zealand **46**:40-65.

Wotton, D. M., and D. Kelly. 2011. Frugivore loss limits recruitment of large-seeded trees. Proceedings of the Royal Society B: Biological Sciences:10.1098/rspb.2011.0185.

Wotton, D. M., and D. Kelly. 2012. Do larger frugivores move seeds further? Body size, seed dispersal distance, and a case study of a large, sedentary pigeon. Journal of Biogeography **39**:1973-1983.

Wotton, D. M., and K. G. McAlpine. 2015. Seed dispersal of fleshy-fruited environmental weeds in New Zealand. New Zealand Journal of Ecology **39**:155.

Yahner, R. H. 1988. Changes in wildlife communities near edges. Conservation biology **2**:333-339.

Young, A., and N. Mitchell. 1994. Microclimate and vegetation edge effects in a fragmented podocarp-broadleaf forest in New Zealand. Biological Conservation **67**:63-72.

Zuidema, P. A., J. A. Sayer, and W. Dijkman. 1996. Forest fragmentation and biodiversity: the case for intermediate-sized conservation areas. Environmental Conservation **23**:290-297.